THE FAUNA OF BRITISH INDIA,

INCLUDING

CEYLON AND BURMA.

PUBLISHED UNDER THE AUTHORITY OF THE SECRETARY OF STATE FOR INDIA IN COUNCIL.

EDITED BY LIEUT.-COL. J. STEPHENSON, C.I.E., M.B., D.Sc., I.M.S. (*ret.*).

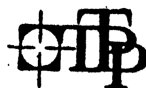
CESTODA.

VOL. I.

BY

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TODAY & TOMORROW'S PRINTERS AND PUBLISHERS
24-B/5, DESH BANDHU GUPTA ROAD,
NEW DELHI-110005

Published by
TODAY & TOMORROW'S PRINTERS & PUBLISHERS

24B/5, Karol Bagh, New Delhi-110005(INDIA)

Printed by
GOYAL OFFSET PRINTERS
308 /6E Shahzada Bagh
DayaBasti, N DELHI-35

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AUTHOR'S PREFACE.

Cestode parasites live in the intestine, and accordingly the digestive tract of the host has to be opened and examined carefully in order to find them. Under the best conditions the search for these worms can hardly be described as agreeable, and in India, where decomposition quickly follows dissolntion, it is frequently very unpleasant.

As many of the cestodes recorded from India by the writer were obtained from animals which had died in the Zoological Gardens, Calcutta, and as these animals had been dead about 24 hours before they were sent for examination, many of the worms unfortunately proved to be in a state of decomposition; consequently it has not been found possible to give an adequate description of some of the parasites dealt with.

Species are here recorded from hosts which do not occur in India, but which were brought to the Zoological Gardens and died there.

The writer has not been able to examine the parasites recorded from India by other helminthologists, and in these cases he has been obliged to rely on the description and figures given by other workers in this field.

He desires to express his thanks to the various authors, editors, and publishers of the several journals named below for their courtesy in allowing the reproduction of certain figures illustrating the anatomy of Indian species, viz.:—The Ceylon Journal of Science (Spolia Zeylanica); Records of the Indian Museum; Journal of the Burma Research Society; The Allahabad University Studies; Parasitology; Quarterly Journal of Microscopical Science; Annals and Magazine of Natural History; Proceedings of the Zoological Society of London; and the Annals of Tropical Medicine and Parasitology, Liverpool.

Special reference is here made to the extensive work done by Professor F. J. Meggitt, of the Zoological Department, University, Rangoon, on the Cestode Fauna of Burma. From his description of species inaccessible to me I have copied freely, and I desire to tender to him my grateful thanks.

In the early part of this year the writer published in Spolia Zeylanica a Monograph on the Order Trypanorhyncha. All the illustrations of the species of this order in the present work are reproduced from that monograph, and I am much indebted to Dr. Joseph Pearson, F.R.S.E., Director of the Colombo Museum, for the loan of the blocks.

A large number of the figures illustrating this volume are original, and are the work of Mr. David Dagnall (of the Liverpool School of Tropical Medicine), Miss E. H. Michie, and Miss Florence Mandley, to all of whom I wish to express my sincere gratitude. I am further indebted to Mr. Dagnall for continuous and very able assistance in a variety of ways during the preparation of this volume.

Mr. A. W. Noel Pillers, F.R.C.V.S., has been good enough to read through the manuscript and proofs, and my thanks are due to him for much friendly advice and useful criticism.

Mr. N. B. Kinnear and Mr. J. R. Norman, of the British Museum (Natural History), have assisted me in the difficult task of correctly naming the birds and elasmobranch fishes respectively, and to them also my thanks are due. It is a pleasure to acknowledge gratefully the extensive, unfailing, and valuable assistance which the Editor has rendered during the passage of the proofs through the press.

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EXPLANATION OF LETTERING.

c., cirrus.
c.m., circular muscle fibres.
c.p., cirrus pouch.
cu., cuticle.
d.e.v., dorsal excretory vessel.
d.v.m., dorso-ventral muscle fibres.
e., eggs.
e.b., excretory bladder.
e.c., egg capsules.
e.v., excretory vessels.
e.v.s., external vesicula seminalis.
f.c., fertilization canal.
f.p., fibrous pad.
g.a., genital atrium.
g.p., genital pore.
g.s., genital sucker.
ip.g., interproglottidal gland.
i.v.s., internal vesicula seminalis.
l., lappets.
l.m., longitudinal muscles.
m.p., medullary parenchyma.
n., nerve.
o., ovary.
o.m., oblique muscle fibres.
ovd., oviduct.
p., parenchyma.
p.g., prostatic glands.
pu.o., paruterine organ.
r.m., retractor muscle.
r.s., receptaculum seminis.
s., spines.
s.c.m., subcuticular muscles.
s.g., shell gland.
sph., sphincter.
t., testes.
t.m., transverse muscle fibres.
u., uterus.
u.d., uterine duct.
u.p., uterine pore.
u.r., uterine reticulum.
u.s., uterine sac.
v., vagina.
v.d., vas deferens.
v.e., vasa efferentia.
v.e.v., ventral excretory vessel.
v.g., vitelline gland.
v.s., vesicula seminalis.
vt.d., vitelline duct.
vu., vulva.
v.u.a., vagino-uterine aperture.

SYSTEMATIC INDEX.

INTRODUCTION.

UNTIL quite recently the only cestodes recorded from India were those found in man and the common domestic animals. The extension of our knowledge of, and interest in, the cestodes of India may be said to date from the time when, in 1902, the late Professor Sir William Herdman visited the Pearl Banks of Ceylon in order to ascertain why these pearl fisheries were so irregularly productive, and, if possible, to suggest remedial measures: Herdman associated pearl formation with the presence of a minute larval cestode which is common in the tissues of the oyster (*Margaritifera vulgaris*).

About the same time Dr. A. Willey, who was then Director of the Colombo Museum, collected some half a dozen species of cestodes in Ceylon, and the late Sir Arthur Shipley published a paper describing these parasites in 'Spolia Zeylanica' in 1903.

In 1906 a much larger collection, apparently obtained by Willey from Ceylon, including trematodes, nematodes, and Acanthocephala was reported upon by Linstow in the same journal.

From 1902 to 1906, Mr. James Hornell obtained a number of cestodes, mostly tetrarhynchids, from the intestines of elasmobranch fishes caught on the Ceylon Pearl Banks. Shipley and Hornell described these parasites in Herdman's 'Report to the Colonial Government on the Ceylon Pearl Oyster Fisheries and Marine Biology,' 5 volumes (1903–1906).

The present writer (1906–1911) extended this work, and issued four reports (Ceylon Marine Biological Reports, 1909–1912) dealing with the marine biology of the Pearl Banks, and incidentally described a considerable number of new species of cestodes.

The cestode fauna of India, up to this date, had not been explored, except that, as noted above, various authors had recorded those cosmopolitan parasites which are found in man and domestic stock.

Between the years 1912 and 1919 the writer studied the cestode parasites of various animals in the provinces of Bengal, and Bihar and Orissa, and published a number of papers

relating thereto in the 'Records of the Indian Museum (1913–1920). These reports represented the first additions to our knowledge of the cestode fauna of British India. Within the last decade several investigators have taken up the study of cestode worms found in India.

Meggitt has devoted attention to Burmese cestodes, whilst Woodland, Moghe, Verma, and Chandler have contributed extensively to our knowledge of the cestodes of the Central and United Provinces.

In addition, the present writer has examined a large number of worms collected in India and brought to England, and has published monographs on the Tetraphyllidea (1925) and on the Trypanorhyncha (1929). The present volume is an attempt to bring together all the information we possess at the present time regarding the cestodes of India. It must, however, be noted that the field is largely unexplored, and it is clear that in the near future additions to our knowledge are likely to be made on a large scale.

Historical and Systematic Account.

The study of worms parasitic in man is of great antiquity, and it is certain that many of them were known and recognized by the most primitive peoples.

In the Egyptian literature there exists a papyrus written 15 centuries B.C. in which is given an account of a disease caused by a worm, the identity of which is, however, quite uncertain. References to parasites, also of uncertain identity, are to be found in the records of other ancient civilizations, including that of India. Amongst the Jews the division of animals into clean and unclean was probably associated with the presence of parasites in the latter, and especially so in the case of the pig. There appears to be good reason for believing that the "plague of fiery serpents" mentioned in the Book of Numbers refers to the guinea-worm. One can therefore safely conclude that the larger tapeworms of man and domestic stock were also known and recognized.

Systematic accounts of these parasites are, however, of a comparatively recent date. It is impossible, and unnecessary, to do more than refer to a few of the more important ones.

Plater, in 1602 (? 1609), dealing with the parasitic worms found in the human body, noted that "they live, feed, and grow like plants, showing neither feeling nor movement, and reach the exterior through the vulva or the anus"; he distinguished, amongst others, "*Lumbricus latus*," which is probably the worm now known as *Dibothriocephalus latus*.

Redi (1684) described certain larval tapeworms from fish; in 1729 he obtained a number of others, and he was probably

the first helminthologist to study these worms from a systematic point of view.

Linnæus (1758) established the genus *Tænia*, and pointed out that a tapeworm "grows at one end and dies at the other." He also stated that each segment has a mouth, but that the animal does not possess a head.

Pallas (1760) dealt with a number of cestode worms from fishes, dogs, and cats. In 1781 he described and figured other cestodes from man and animals.

Goeze (1782) published a valuable book, with 44 plates, in which he described and illustrated certain cestodes from dogs cats, horses, sheep, rabbits, squirrels, mice, rats, ducks, crows, and various fishes. In this work the tapeworms were all included in the genus *Tænia*, of which he recognized two subdivisions, viz., "*T. viscerales*" (cystic forms) and "*T. intestinales*" (adult worms). He discovered the head in *Tænia echinococcus*, the embryo in the egg of *Tænia canina* (*Dipylidium caninum*), and he also made important observations on the development of Cysticercus fasciolaris. His opinion was that all intestinal worms were inherited.

Bloch (1779) gave an account of a number of cestode parasites in certain fishes and birds. In 1788 he wrote a paper, illustrated with 10 plates, on the development and treatment of intestinal worms, and he dealt with a number of species from fish, birds, cats, sheep, etc.

Fabricius (1780) described other cestodes from fishes.

Abildgaard (1790) published a paper dealing with certain tapeworms found in birds and fishes, and he noted that in one segment of a tapeworm obtained from a dog there were no less than 140,000 eggs.

Zeder (1800) gave 'A First Account of the Natural History of the Tapeworms,' and in his work he placed the helminths in five classes. In 1803 he produced a book in which the adult cestodes were divided into four families and the cystic forms were distributed in five other families.

Rudolphi (1809–1810) proposed the first extensive scheme of classification of the parasitic worms, which he divided into five orders, viz. :—

1. Nematoidea, including *Filaria*, *Ascaris*, etc.
2. Acanthocephala, comprising two genera only, viz., *Echinorhynchus* and *Tetrarhynchus*.
3. Trematoda.
4. Cestoidea, including six genera only, viz., *Scolex*, *Caryophyllæus*, *Ligula*, *Tricuspidaria*, *Bothriocephalus* and *Tænia*.
5. Cystica, with three genera only, viz., *Cysticercus*, *Cœnurus*, and *Echinococcus*.

In 1819 he reclassified them as follows, and at the same time defined the various orders and genera, viz. :—

Order 1. Nematoidea.
,, 2. Acanthocephala.
,, 3. Trematoda.
,, 4. Cestoidea.

Genera :—*Caryophyllæus*, *Scolex*, *Gymnorhynchus*, *Tetrarhynchus*, *Ligula*, *Triænophorus*, *Bothriocephalus* (*Dibothrius*, *Tetrabothrius*, *Onchobothrius*, *Rhynchobothrius*), *Tænia*.

Order 5. Cystica.

Genera :—*Anthocephalus*, *Cysticercus*, *Cœnurus*, *Echinococcus*,

and *Entozoa dubia*.

The work done by Rudolphi was remarkable in every way. Following the line of investigation suggested by the above author, Blainville (1828) proposed a classification which differed in many respects from that of his illustrious predecessor.

Dujardin (1845) gave a very full and excellent account of the worms in question, extending and amplifying the scheme of classification propounded by Rudolphi.

Van Beneden (1850) studied the cestodes in particular, especially those from marine fishes. He erected many new genera and species, and of the latter he gave very full descriptions and good illustrations. He recognized four orders, viz., Tetraphylles (=Tetraphyllidea Carus, 1863), Diphylles, Pseudophylles (=Pseudophyllidea Carus, 1863), and Aphylles or Téniens.

Diesing (1850, 1854, and 1863) published most elaborate and lengthy systematic accounts of the Cestoda ; large numbers of tribes, subtribes, sections, orders, genera, and species were erected, almost all of which have since fallen into synonymy.

Carus (1863) divided the class Platyelminthes Vogt into three orders, viz., (*a*) Turbellaria, (*b*) Trematodes, and (*c*) Cestodes. The latter order he subdivided into five families, viz. :—

Caryophyllidea, Tetraphyllidea, Diphyllidea, Pseudophyllidea, and Tæniadea (Diesing) van Beneden (Cyclophyllidea van Beneden),

with the single genus *Tænia* (L.) Rudolphi, containing the following subgenera :—

(*a*) Cysticæ (larva a cysticercus).

(1) *Cystotænia* R. Leuckart.
(2) *Echinococcifer* Weinland.

(*b*) Cysticercoideæ (larva a cysticercoid).
(1) *Hymenolepis* Weinland.
(2) *Dipylidium* R. Leuckart.

He also mentions the following of uncertain subgeneric rank:—*Liga* Weinland, *Tetracampos* Wedl, *Lepidotrias*, *Dilepis*, *Proteocephalus* Weinland, *Alyselminthus* Zeder (*Halysis* Zeder).

Monticelli in 1892 placed together in a group which he called Cestodaria all those cestodes in which the body was unsegmented and contained a single set of genital organs; such forms are now frequently referred to as monozootic cestodes, in contradistinction to other species, the bodies of which are made up of numerous segments each containing one or more sets of genital organs, and which are known as the polyzootic cestodes.

Braun (1894–1900) raised the cestodes to a class, and divided them into the following five orders, viz.:—

(1) Pseudophyllidea Carus, 1863.
(2) Tetraphyllidea Carus, 1863.
(3) Cyclophyllidea van Ben. (*sic*), this being a synonym of Tænioidea Zwicke, 1841, Diesing, 1850.
(4) Diphyllidea Carus, 1863.
(5) Trypanorhyncha Diesing, 1863.

Lühe (1910) divided the class Cestoda as follows:—
In addition, he quoted nine genera which he found it impossible to refer to any of the above orders.

A. Cestodaria.
B. Rhynchostomida (these have since been proved to be trematodes).
C. Cestodes, s. str., with the four orders Pseudophyllidea Carus, 1863; Trypanorhyncha Diesing, 1863; Tetraphyllidea Carus, 1863; and Cyclophyllidea (? van Ben.) Braun, 1900. This scheme of classification is accepted by Meggitt, 1924, who placed each of Lühe's divisions in a separate subclass.

Poche (1926) proposed the following entirely new scheme of classification, which differs widely from that suggested by Braun and adopted by Lühe, Meggitt, and other authors:—

Class Cestoidea.

Subsubclass I. Amphilinoinei.

Order 1. Amphilinidea.
2. Gyrocotylidea.

Subsubclass II. Tænioinei.

Order 1. Bothriocephalidea.
2. Echinobothriidea.
3. Tetrarhynchidea.

Suborder 1. Haplobothriinea.
2. Tetrarhynchinea.

Order 4. Tæniidea.

Suborder 1. Phyllobothriinea.
2. Tæniinea.

Thus the entire class Cestoidea is divided into two subsubclasses (*sic*), the first (Amphilinoinei) containing a small number of forms, whilst the second subsubclass (Tænioinei) includes all the rest of the cestodes. Poche unites in his order Tæniidea the entire orders Cyclophyllidea and Tetraphyllidea, calling the latter suborder Phyllobothriinea and the former suborder Tæniinea.

Woodland (1927) proposed a revised classification of the order Tetraphyllidea which differed widely from that of Poche on major points, for, whilst Poche unites the orders Cyclophyllidea and Tetraphyllidea into one order (Tæniidea)—retaining the order Trypanorhyncha (Tetrarhynchidea),—Woodland unites the Trypanorhyncha and the Tetraphyllidea (together with Proteocephalidæ) into one order Tetraphyllidea, keeping the order Cyclophyllidea distinct. He thus divides the Cestoda into the three orders Pseudophyllidea, Cyclophyllidea, and Tetraphyllidea.

Pintner (1928) suggested the following systematic arrangement of the order Cestoidea Rudolphi, 1809 :—

Order 1. Amphilinidea.

Families :—Amphilinidæ, Gyrocotylidæ.

Order 2. Cestodes, s. str.

Families :—Bothriocephalidæ, Echinobothriidæ, Tetrarhynchidæ, Tetraphyllidæ, Proteocephalidæ, Tæniidæ, Discocephalidæ, Tetragonocephalidæ, Cephalobothriidæ, Balanobothriidæ.

The first order comprises the monozootic and the second order the polyzootic cestodes. With reference to the latter order, it will be seen that all the four old orders, viz., Pseudophyllidea, Cyclophyllidea, Trypanorhyncha, and Tetraphyllidea, are merely reduced to the rank of families, and are referred to as Bothriocephalidæ, Tæniidæ, Tetrarhynchidæ, and Tetraphyllidæ respectively.

The old family Lecanicephalidæ is split up into three new ones, and a new family, Discocephalidæ, is formed for the reception of the genus *Discocephalum*, which contains only a single species.

It will thus be seen that within the last five years the classification has been undergoing rapid and profound changes, and at the present time the greatest diversity of opinion exists regarding even the broad lines on which these worms should be systematically arranged; so much so that hardly any two authorities are agreed on the matter.

Any investigator who has devoted much time and thought to the study of any particular group of animals will have recognized clearly, and probably painfully, that a satisfactory system of classification is a matter of great difficulty, even if it is not altogether impossible. The reason why this is so is very obvious. In nature, the hard-and-fast distinctions which are arbitrarily drawn by naturalists between species, genera, families, orders, classes, and even phyla, rarely exist. Like the boundaries between counties, states, and countries, they are usually artificial. It is but reasonable to realize and admit a simple and evident fact, viz., that the forms of life are very plastic, very diversified, and frequently merge into each other by almost imperceptible gradations, with the result that no system of classification can possibly be entirely adequate. The utility of a good scheme of classification lies in the fact that it enables us broadly to classify our knowledge and identify species.

The usual four orders of cestodes have the following characters:—

(1) Cyclophyllidea, embracing forms in which the head bears four suckers (*acetabula*), and in which the vitelline glands are condensed into a single mass, usually behind the ovary.

(2) Pseudophyllidea, including those species in which the head bears two sucking grooves or *bothria*; in which the acini of the vitelline glands are scattered throughout the parenchyma; and in which a uterine pore, normally opening on the ventral surface, is usually present.

(3) Trypanorhyncha, containing species in which the head bears four protrusile *proboscides* armed throughout their length with minute spines and retractile within a cylindrical sac situated in the posterior part of the head.

(4) Tetraphyllidea, in which the head consists of four ear-like lappets or *bothridia* whose surfaces may or may not be split up into *areolæ*, and which may be armed anteriorly with hooks.

These orders are differentiated in a general way on the characters of the scolex. The tendency amongst modern systematists is to discount the value of external features and to base the classification on internal anatomical details. It would appear, however, that the head is as important and as necessary a part of the anatomy as, say, the muscular system, and as useful systematically. Throughout the entire animal

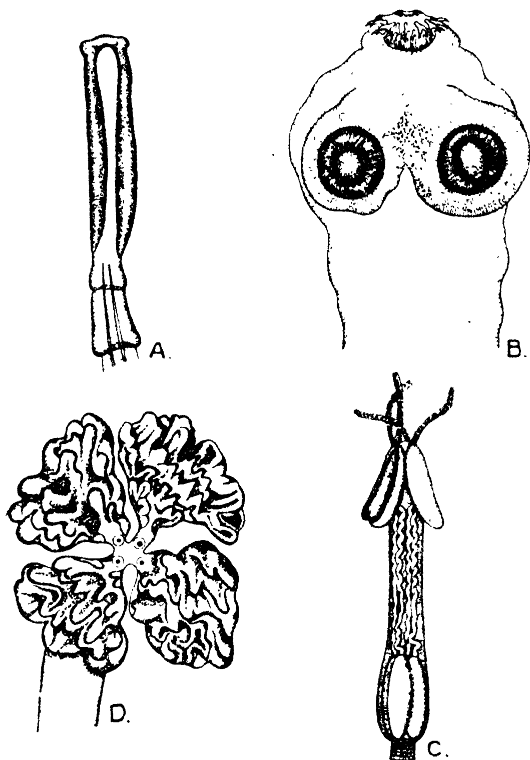


Fig. 1. Diagram representing the scoleces in the superfamilies: A, Dibothriocephaloidea; B, Tænioidea, C, Tetrarhynchoidea; and D, Phyllobothrioidea. (Original.)

kingdom the broad schemes of classification rest in a very large measure on external characters. Schneider in 1866 attempted to classify the Nematōda on certain peculiarities of the muscular system. His scheme is now wholly discounted, because it was found that worms closely related to each other in every other way were nevertheless widely separated when classified on the muscular system; other worms, as widely

different as possible from each other, yet had a certain type of muscular system in common; whilst yet others combined two types of muscular system in one individual. The head is of considerable taxonomic value, and, although it shows a little variation, every other organ will also be found to vary. The head, being so easy to examine, is consequently, in the writer's opinion, of considerable importance.

Turning to the classification of the Cyclophyllidea, one finds that the only character common to the various species and genera of the family Anoplocephalidæ is the fact that they have an unarmed head. The essential feature of the family Davaineidæ is the presence of a large number of extremely small hammer-shaped hooks on the rostellum. In the family Tæniidæ the head is usually armed with a double crown of hooks, and the uterus, in practically all species, consists of a central stem which bears a number of compound lateral branches on each side. In species of the families Acoleidæ and Amabiliidæ a vaginal pore is absent; and the essential points of difference between these two families are that in the former the musculature consists of at least two layers of longitudinal fibres alternating with three layers of transverse fibres, and the cirrus is always very large and generally armed with very strong hooks; in the latter family the musculature is relatively feeble and the cirrus is not armed. The family Mesocestoidiidæ is characterized by the genital pores being situated on the flat ventral surface. The characters distinctive of the family Tetrabothriidæ are an unarmed head, the suckers of which usually carry anterior appendages, and the position of the vitelline glands, which are situated anteriorly to the ovary.

It will be noted, therefore, that the form of the head has been considered of sufficient importance to separate off at least the four families Anoplocephalidæ, Tetrabothriidæ, Davaineidæ, and Tæniidæ. On the other hand, we find that the presence of a double set of genital organs in some forms is only considered as a generic character, as, for instance, in *Dipylidium*, *Moniezia*, etc. Further, in *Dioicocestus* the sexes are separate (*i. e.*, some strobilæ contain only male and others only female organs), and this character has hitherto been accepted by all as merely a generic distinction. Lastly, the occurrence of paruterine organs in some species ranks, in our present schemes of classification, as a subfamily character.

Sufficient has been said to indicate that whilst certain characters have been considered adequate to define a family, other—and what appear to be more important—characters only rank as of generic, and sometimes even only of specific, value. This lack of uniformity probably arises from three causes, viz.: (1) that different investigators have different

opinions as to the relative value of particular morphological characters; (2) that no thought or attention is given to the relative value of these characters; and (3) that the relative value of any particular character can only be adequately assessed by investigators after they have acquired a prolonged, varied, and practical experience of the forms they are classifying.

It will doubtless be agreed that amongst the cestodes, as amongst all other animals and plants, any particular organ will vary within wide limits in the different species, and it is this fact which makes the classification so extremely difficult and so admittedly artificial. If such variations did not exist, systematic zoology would be simple. Knowing that they do occur, it is not surprising that schemes of classification not based on extensive acquaintance with numerous living forms are found wanting when tested by the bewildering variety which occurs in nature.

If, for example, we included in one genus, or in one family, all those species in which the genital pores are unilateral, or if we included in another genus or family those species in which paruterine organs develop; or again, if we united those species in which the head was armed with hooks, or those species in which the ovary is situated asymmetrically, then in each of the above cases we should be classifying together worms which are admittedly very different from each other. Thus the species with unilateral pores include *Anoplocephala*, *Hymenolepis*, etc.; those with paruterine organs *Stilesia*, *Metroliasthes*, *Paruterina*, etc.; those with armed heads *Tænia*, *Davainea*, and most species of *Hymenolepis*, etc.

Lastly, let us suppose, using one character as an instance, that the muscular system of a species of *Dibothriocephalus* (Pseudophyllidea) was found to be identical with that of a species of *Tænia* (Cyclophyllidea), and also with that of a species of *Phyllobothrium* (Tetraphyllidea). We should be obliged to place these three species together because they have a common type of muscular system. Clearly the result would be chaos. Nevertheless, it is a fact that some species in each of the three above-named orders have an identical muscular system. The matter is of importance, because it has recently been stated that the muscular system is of one type in the Tetrarhynchidæ, of another type in the Tetraphyllidæ, and of still another in the Proteocephalidæ.

The arrangement of the muscular system is certainly more difficult to determine than is the form of the head; and, further, it varies widely in different parts of an individual worm. It is not evident what advantage is gained by changing the basis of classification, but the disadvantages are very obvious. If we suppose it to be true that the above three groups do actually

possess a different type of muscular system, as has been stated to be the case, then this fact strengthens the ground for believing that the head, which is so different in each group, is as important in diagnosis as any other organ.

It will thus be clear that any particular morphological character varies within wide limits, and has only a relative importance. Cestodologists have yet to agree whether a head is more important than a pore, a hook more reliable than a particular type of muscular system, or a paruterine organ more valuable than an asymmetrically placed ovary, etc., from a taxonomic point of view. No agreement has yet been reached on fundamental principles of this nature, and the result is that great diversity of opinion exists as to the relative value of any particular morphological feature.

Woodland considers that scolex characters count for very little, and that a more satisfactory scheme of classification would result, at least so far as the orders Tetraphyllidea and Trypanorhyncha and the family Proteocephalidæ are concerned, if more attention were paid to the form of the ovary in transverse sections, the position of the vagina relative to the uterine sac, and the distribution of the vitellaria and longitudinal muscles.

The writer has up to the present accepted in its broad application Braun's classification, in which the cestodes are considered as a class divided into the four orders Pseudophyllidea, Tetraphyllidea, Trypanorhyncha, and Cyclophyllidea.

After a long and careful consideration of the various schemes of classification which have been proposed from time to time, and which are indicated above, he is now thoroughly convinced that it is undesirable to retain the above four orders in their present application, and a new scheme of classification, differing only in minor points from that proposed by Pintner in 1928, is adopted in this volume, full details concerning which are given on page 6.

General Account of the Cestodes.

Worms of this class are all internal parasites, and they are rarely found outside the intestine. *Stilesia hepatica*, however, occurs in the liver and bile ducts, and *Nematotænia dispar* has been recorded from the pericardial sac of the frog.

Head or Scolex.—It is by means of this organ that the worm fixes itself to the wall of the intestine. In some cases (*Stilesia globipunctata*, *Davainea echinobothrida*, etc.) the head lies deeply buried in the mucosa, giving rise to very definite pathological changes. The head is usually a conspicuous organ except in the monozootic cestodes and in *Ligula*.

In the Cyclophyllidea it bears four muscular cup-shaped suckers which are referred to as acetabula. Hooks may also be present, the shape and size of which vary within wide limits. They are usually borne on a retractile projection called the rostellum, which is situated on the anterior aspect of the head. In addition, the four suckers are sometimes armed with deciduous spines. In other cases the entire cuticle covering the head and the anterior part of the strobila may also be armed with minute spinules. Folds of tissue may develop on the posterior part of the head or on the suckers. Occasionally the head is lost, and in its place a pseudoscolex develops, which, in the genus *Fimbriaria*, is very large and conspicuous.

The tetraphyllidean head in the two families Phyllobothriidæ and Onchobothriidæ consists typically of four ear-like outgrowths or lappets. In some species these lappets, which are called bothridia, are simple ; in others they are modified in various ways. One or more suckers may develop on the face of the bothridium, or its entire surface may be split up into loculi by one or many transverse and longitudinal septa. At its anterior extremity each may bear spines, the shape of which varies considerably. Each bothridium may be borne on a stalk, when it is said to be pedunculated, or the stalk may be absent, when it is referred to as sessile.

In the family Proteocephalidæ the head closely resembles the cyclophyllidean scolex in that it bears four suckers. The entire cuticle covering the head, and in some cases that of the anterior part of the strobila, may bear minute spinules. In the genus *Gangesia* a rostellum is present, armed with spines.

In the Pseudophyllidea the head consists typically of two boat-shaped sucking grooves called bothria. In some instances the margins of each bothrium fuse, giving rise to a tubular or conical organ, as in *Duthiersia* and *Bothridium*. Occasionally the bothria are replaced by a terminal fixation organ or by a pseudoscolex, and accessory sucking organs may also be present. In a few cases the head is armed with hooks.

In the order Trypanorhyncha the head typically carries four long thread-like proboscides armed with hooks of the most diverse shape, each proboscis being retractile within an elongated, somewhat cylindrical sac which is situated in the posterior part of the head. In addition, the head bears either two or four bothridia. In a larval (?) trypanorhynchid recently described from America the worm possessed four protrusile, unarmed proboscides, and, as far as can be ascertained, no accessory bothria or suckers were present.

In the monozootic cestodes the head as such may be said to be absent, but in some species sucking organs are developed.

Attention is called elsewhere to the fact that the posterior part of the head is, when once established in the final host, a proliferating area from which segments are being continuously budded off.

Neck.—This name is applied to the unsegmented zone which is found in some cestodes immediately behind the head.

Strobila.—The strobila is the general body of the worm ; it is composed of a chain of *segments* or *proglottides*, except in the monozootic species.

Proglottides.—These vary very greatly in shape and size not only in different species, but even in the same individuals. The worm may be composed entirely of shallow segments, *i. e.*, segments in which the transverse diameter is considerable and the antero-posterior diameter extremely small ; they are then said to be *linear*. In other cases the mature or gravid segments may be longer than broad ; the lateral margin of the segment may be straight or convex ; the posterior margin of each segment may overlap the anterior margin of the succeeding segment, in which case they are referred to as being *imbricated*. The term *fimbriated* or *laciniated* is applied when the posterior margin overlapping the next segment is ragged. Sometimes it is only the lateral posterior edges of each segment which overlap the next segment ; they are then called *salient*. In some species of Pseudophyllidea and Trypanorhyncha each primary segment divides into two or more secondary segments. Most species of cestodes are flat and delicate, but a few are fleshy. The ventral side of the worm is that nearest to the ovary ; consequently it can only be determined in the majority of forms by making transverse sections, but when a uterine pore is present it is usually ventral.

Cuticle.—In the Cestoda the cuticle is a thin covering, resistant and elastic, which may bear minute spines, hairs or tubercles.

Parenchyma.—The bulk of the body of a cestode worm is composed of connective tissue which is known as the parenchyma. It fills up all interstices of the worm and is typically divided by the circular muscular fibres into two zones, namely, the cortical parenchyma and the medullary parenchyma. Usually the essential genital organs are situated in the medullary parenchyma, and the longitudinal muscles, nerves, and excretory vessels in the cortical parenchyma.

Calcareous Corpuscles.—These consists of refractile bodies, often spherical, composed of carbonate of lime, and measuring from 5 to 25 μ ; they are found most frequently in the cortical parenchyma. In some species they are much more abundant than in others. They appear to originate as concretions within certain parenchymatous cells which eventually atrophy, and, as a result, they are often found free in the tissue.

Nervous System.—This consists of ganglia situated in the head which give off nerves to the suckers, and from which a number of longitudinal nerves pass backward through the whole length of the worm. These are connected together by numerous anastomoses. Of these longitudinal nerves the principal are two large lateral nerves, one on each side, situated external to the muscular system.

Excretory System.—This commences in excretory cells called "flame cells." Each is provided with numerous processes which ramify in the parenchyma; they are hollow, the cavity being drained by a minute capillary, and bearing a tuft of vibratile cilia which in life exhibits a flickering motion. Numbers of these cells are scattered throughout the parenchyma, especially in the cortical zone. The minute capillaries arising from the flame cells anastomose, and uniting together form eventually, as a rule, four main longitudinal vessels (ten in *Hymenofimbria*), two running along each lateral margin of the segment, one dorsal and one ventral; these open into a minute vesicle situated at the end of the last segment. When once the latter has been shed, the vessels merely drain posteriorly. Very frequently the ventral vessel is larger than the dorsal one, although exceptionally the reverse may be the case. The dorsal vessel may lie immediately dorsal to the ventral, or lateral or median to it. In some species the dorsal vessel may be absent altogether, or may be present only in the anterior part of the worm, as in certain species of *Avitellina*. The genital ducts, viz., the vagina and the vas deferens, may pass dorsally to both vessels, between them or ventral to them.

In many species of Pseudophyllidea the excretory vessels cannot be seen even in transverse sections; in some other species they are very small and difficult to see.

Muscular System.—In the various orders great diversity exists in the arrangement of the muscular system. It usually consists of longitudinal, circular, and diagonal or dorso-ventral fibres. In the Cyclophyllidea the longitudinal muscles are typically disposed in single bundles which are sometimes continuous throughout the body. Internally to them are the circular fibres which, as noted above, divide the parenchyma into cortical and medullary parts, the former being situated externally to the circular fibres, whilst the latter lies internally to them. Occasionally the longitudinal bundles are in two, three, or four layers, with circular fibres between each layer. The diagonal fibres are, as a rule, small and ill-defined. In gravid segments the musculature atrophies, as a result of which the segments not only break loose from the chain, but also rupture easily, thus liberating the eggs.

Genital Pores.—The aperture by means of which the vas

deferens communicates with the exterior is called the male genital pore, whilst the opening of the vagina to the exterior is called the female genital pore.

In the Cyclophyllidea, Tetraphyllidea, and Trypanorhyncha the uterus is almost always, but not invariably, a closed sac. The male and female genital pores practically always open close together, very frequently in a common genital atrium, which communicates with the exterior by a single aperture. The uterine opening, when present, is always distinct from the male and female genital openings. With very few exceptions the opening of the male and female genital organs is situated laterally in the three orders mentioned above, and also in some families of the Pseudophyllidea, viz., Amphicotyliidæ, Triænophoridæ, and Echinophallidæ.

In the Cyclophyllidæ uterine pores are absent, but in the genus *Mesocestoides* both the male and female pores are situated on the flat (ventral) face of the segment. When a uterine pore is present it is usually to be found on this surface, but in some cases it is situated dorsally, as in species of the family Ptychobothriidæ. When the male and female genital pores are on the lateral margin of the segment they may all open on the same side of the strobila, in which case they are said to be *unilateral*, as in species of *Hymenolepis*. In other species the pores open regularly to the left and to the right in succeeding segments: they are then said to be regularly alternate, as in species of the genus *Leptotænia* etc. In other cases they are disposed irregularly on each side of the strobila, and they are then said to be *irregularly alternate* as in *Tænia* spp. etc. The position of the pore in each segment varies in different species; it may be situated anywhere on the lateral margins of the segment; in some cases it is placed slightly dorsally or ventrally, when it is said to be subdorsal or subventral.

Genital Organs.—In the new order Dioicocestidea the sexes are separate, *i.e.*, some strobilæ contain only male and others only female genital organs. This condition is unique in the class Cestoda; in all other genera the worms are hermaphroditic, *i.e.*, each mature segment contains both male and female genital organs. In the vast majority of tape-worms a single set of genital organs is present in each mature segment. Usually the male genital organs mature before the female, and in some species this condition is so pronounced that a relatively considerable portion of the anterior part of the strobila contains male genitalia only. In some species a double set of genital organs is present in each segment (*Dipylidium*, *Moniezia*, etc.).

In the family Fimbriariidæ the reproductive organs are apparently not arranged segmentally. In the genus *Triplotænia* there is one ovary, yolk-gland, testis, and vagina, but

four or five cirrus pouches in each lateral half of the segment. In the genera *Diploposthe* and *Amabilia* every mature segment contains a single set of female genital organs, with a cirrus pouch at each lateral margin.

It will therefore be seen that considerable diversity exists in the arrangement of the genital organs.

The monozootic cestodes may be considered as consisting of a single segment bearing weak fixation organs anteriorly and containing a single set of genital organs.

In the pseudophyllidean genus *Ligula*, and in a few other cyclophyllidean genera (*Parvirostrum* etc.), although the genital organs are segmentally arranged, the corresponding segmentation of the strobila is very indistinct.

Segments in which the genital organs are not developed at all, or only partly developed, are said to be *immature*. Those in which they are fully developed and functioning are *mature*, and those in which the uterus contains eggs are *gravid*.

It must be clearly understood that the anatomy of a segment varies considerably in parts of the same strobila. As the growth of the worm is from the head backward, those segments at the anterior end of the strobila are the youngest and those at the posterior end the oldest. The result is that the anterior proglottides present degrees of development from the stage in which it is impossible to distinguish even the rudiments of the genitalia to that in which these organs are fully developed.

Male Genital Organs.—The plan on which these organs are arranged is the same throughout the entire class Cestoda, the differences which exist being limited to minor details (fig. 2).

Testes.—The testes are usually very numerous and situated dorsally in the medulla, but in the genera *Monticellia*, *Rudolphiella*, *Marsypocephalus*, and *Amphicotyle* they lie in the cortex. In certain species of Tetraphyllidea and Trypanorhyncha the mature segments contain a number of fibrous capsules, in each of which there are five or six testes. In the genera *Aploparaksis*, *Diorchis*, *Hymenolepis*, and *Oligorchis* each mature segment contains one, two, three, and four testes respectively. In some species of *Tænia* each mature segment contains about 500 testes, and in some other genera the number is even greater. They may lie along the lateral margins of the segment, in which case they are said to be in two fields; in other species they lie posteriorly to the ovary; in yet others anteriorly; and in still other species they may surround it. They may be confined to the space between the excretory vessels, or they may extend laterally to them.

From each testis a vas efferens arises. It is so minute that, except in some species of *Hymenolepis*, *Stilesia*, etc., it is rarely seen even in sections. The vasa efferentia unite into a common duct called the vas deferens; usually this duct is much coiled, and it runs to the genital pore. The terminal part of the vas deferens (the cirrus) is surrounded by a muscular organ called the cirrus sac; this is usually small, but in many species of *Hymenolepis* it is a very conspicuous structure, extending almost across the entire breadth of the segment. This muscular pouch is concerned in the protrusion and retraction of

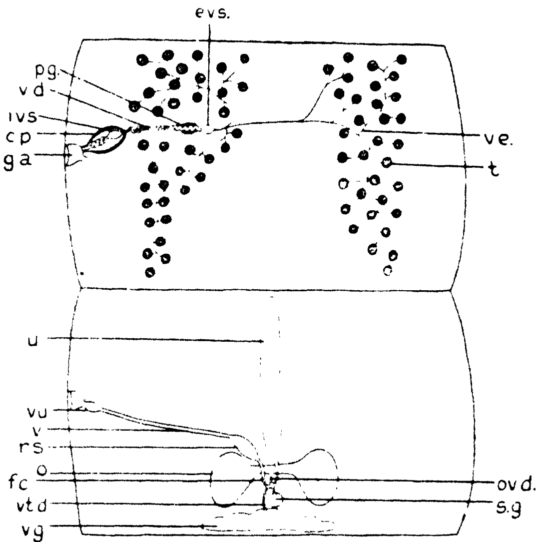


Fig. 2. Diagram representing the male and female genitalia of a Tænioidean cestode. (Original.) For explanation of the lettering on this and other figures see p. xxvii.

the terminal part of the vas deferens: this usually lies coiled within the cirrus sac, is often modified, and may be covered with minute spines. Owing to the fact that the male and female genital organs may mature at different times in the same strobila, receptacles are developed on the vas deferens for the storing of spermatozoa; such a dilatation is called a seminal vesicle. When it develops on any part of the vas deferens situated outside the cirrus sac, it is called the external seminal vesicle, whilst when it develops on any part lying within the sac it is referred to as an internal seminal vesicle. In some species a seminal vesicle is entirely absent, in others one vesicle is present, whilst in yet other species there are two.

Occasionally a portion, or the whole, of the vas deferens may be covered with glandular cells to which the name prostate gland has been applied. The relation of the cirrus to the terminal part of the vagina is often a point of some importance ; the sac may be anterior throughout the entire strobila ; in other cases its position varies even in one strobila, it being situated anteriorly in some segments and posteriorly in others.

The cirrus sac may also be dorsal or ventral to the terminal part of the vagina. Here again in some species it is always either dorsal or ventral, whilst in others it is sometimes dorsal and occasionally ventral even in the same strobila.

Female Genital Organs.—The female genital organs consist of an ovary which discharges eggs into an extremely fine oviduct ; the latter branches into two larger ducts ; one, called the vagina, leads to the genital pore, and the other, named the uterus, becomes filled with eggs, and may or may not open to the exterior. In addition, two glands, the vitelline and shell glands, discharge their secretions by means of ducts into the oviduct ; the latter is, however, not invariably present (fig. 2).

Ovary.—Except in the genera *Monticellia* and *Rudolphiella*, the ovary is invariably situated ventrally in the medullary parenchyma. In the vast majority of species it is bilobed or butterfly-shaped, the two lobes being united by a narrow isthmus. In some species (and, according to Woodland, in all Phyllobothriidæ and Tetrarhynchidæ) the organ is bilaminate, *i.e.*, it consists of two dorsal lobes and two ventral lobes united in the middle. In other species it is apparently a single, more or less globular or oval organ. It may be situated in front of or behind the testes, or, as noted above, it may be surrounded by testes. Also it may occur either in the posterior, middle, or anterior part of the segment, and in some species it is situated asymmetrically, usually in that half of the segment in which the pore occurs. In species which possess double genitalia there are two ovaries in each segment, one on each side.

Vagina.—From the genital pore, whether this is situated on the lateral margin or on the ventral surface, the vagina runs, usually, in a slightly curved course to the ovarian isthmus. A short portion of the vagina near the pore is sometimes dilated, as in the genera *Stilesia* and *Avitellina*, and this is referred to as the vulva.

Near the ovarian isthmus the vagina often dilates, and such a vesicle is called a receptaculum seminis ; it functions in storing spermatozoa until they are required.

In the families Acoleidæ and Amabiliidæ, and also in the genus *Aporina*, a vaginal pore is said to be lacking. In the former family the cirrus is armed with strong spines, and

apparently penetrates the tissues during copulation. In the genus *Tatria* the distal end of the vagina, instead of opening to the exterior, turns backward into the next following segment, and opens into the receptaculum seminis of that segment.

Oviduct.—From the ovary a short minute duct—the oviduct—arises; ova discharged from the ovary pass along this channel and are fertilized in its proximal part. For this reason this portion of the oviduct is called the *fertilization canal* or *oötype.* Near its origin there is sometimes a small muscular dilatation called the *egg-swallowing apparatus*, which is concerned in the propelling of the ovarian cells forward. The ducts from the vitelline glands, when these are present, and from the shell gland, when this is present, discharge their contents into the fertilization canal. The distal part of the oviduct is continuous with both the vagina and the uterus; the two latter organs may, for the sake of simplicity, be considered as the two limbs of the letter U, the oviduct opening in the middle of the basal curvature. As we have noted above, the vagina runs to and opens at the genital pores. The uterus will be considered later.

Vitelline Glands or Yolk-glands.—Great diversity exists with respect to the arrangement and disposition of these glands. In the Cyclophyllidea the acini are condensed into a single gland, which, as a rule, is placed posteriorly to the ovary; it is always situated in the medulla. In species possessing double female genital organs the vitelline glands are also duplicated. In the genera *Stilesia*, *Avitellina*, and *Thysanosoma*, the glands are entirely absent, whilst in the genera *Ascotaenia* and *Thysaniezia* they are rudimentary.

Lühe (1910) and Meggitt (1924) state that the vitelline follicles in the order Tetraphyllidea are situated in the cortex. The writer found them external to the longitudinal muscle layer in the genera *Thysanocephalum* and *Pedibothrium*. In the genera *Tylocephalum*, *Cephalobothrium*, and *Balanobothrium* they lie internally to the longitudinal muscles, whilst in *Adelobothrium* they are intermingled with the longitudinal muscle bundles. Woodland (1927), however, states that they are situated in the medulla. All authorities agree that the glands are usually in two lateral strands, although in some species they develop an annular arrangement in the posterior segments. In the genera *Monticellia* and *Rudolphiella* they are definitely in the cortex. Cooper (1918) stated that the glands were mostly cortical, seldom medullary, in the Pseudophyllidea. He figured them as being external to the longitudinal muscles in *Bothriocephalus claviceps*, *B. cuspidatus*, and other species, and internally to the muscles in *Abothrium rugosum*. Nybelin (1922), in his monograph on the Pseudophyllidea, figured the glands as being external to the longitudinal muscles in three

species of *Eubothrium*, whilst in other species of this genus they are intermingled with the muscles. In the genera *Parabothrium*, *Abothrium*, and *Priapocephalus* they are external to the longitudinal muscles. In some genera they encircle the segments, whilst in others they are restricted in position to two narrow, longitudinal, lateral tracts.

Our knowledge as to the position of these glands in the order Trypanorhyncha is not sufficient to justify us in making a definite statement, but in all the species that have been studied they are situated in the medulla, although it is true that in most of these species the division into a cortical and medullary parenchyma is ill-defined. It is, however, definitely known that they almost always encircle the segment, but in some species their distribution is certainly limited to the lateral margins of the segment.

In the monozootic cestodes the vitelline glands are apparently situated in the medulla, and consist of two lateral tracts.

Shell gland.—The function of this organ (which is always small) is unknown. It received its name because the early helminthologists were of opinion that it was concerned in the formation of the shell; it is now known that it does not form the shell. The gland is usually situated close to, and posterior to, the ovary, but occasionally it appears to consist of a ductless glandular thickening on the wall of the fertilization canal. In some species it appears to be entirely absent.

Uterus.—The structure and form of the uterus varies within wide limits in different species. Amongst the Cyclophyllidea, in forms like *Hymenolepis* spp., it usually consists of a transverse sac (with lobulated walls) which entirely fills the segment. In most species of *Tænia* it is a central stem with a number of lateral compound branches on each side. In species of *Dipylidium* it is composed of a reticular network in the interstices of which capsules occur; each of the latter contains one or more eggs. In the family Davaineidæ the uterus, as such, disappears, and is replaced by parenchymatous capsules. These may be globular, oval, or polygonal, and each may contain one or several eggs. In certain other cestodes the uterine walls disappear, and the eggs apparently lie free in the parenchyma. In species of the genera *Stilesia*, *Avitellina*, *Thysanosoma*, *Ascotænia*, *Thysaniezia*, *Metroliasthes*, *Biuterina*, *Idiogenes*, *Culcitella*, and *Rhabdometra* the uterus is replaced by one or more fibrous capsules (par-uterine organs) into which the eggs pass.

In the Cyclophyllidea the uterus does not open to the exterior; the eggs are liberated by the disintegration and rupture of the cortical parenchyma of the segment. In at least one species of *Avitellina* the eggs are discharged into the longitudinal excretory vessels.

The essential genital organs gradually atrophy as the uterus develops, so that in fully gravid segments no trace of them is to be found, and the segment becomes practically a bag of eggs.

In the Pseudophyllidea the uterus usually consists of a convoluted tube which in some species assumes the form of a rosette. In the family Amphicotylidæ it is sac-like, and in a few species of this order the uterine wall apparently disappears and the eggs lie free in the medullary parenchyma. In almost all species the uterus opens to the exterior by means of a pore, which in some families is marginal (Amphicotylidæ and Triænophoridæ); in one family (Echinophallidæ) it is submarginal, in *Ptychobothrium* it is dorsal, whilst in all the other families of this order the uterine pore is ventral, *i. e.*, situated on the flat side of the segment. It is to be noted that in this order the essential organs do not atrophy as the uterus develops; this constitutes a difference from the Cyclophyllidea.

In the Tetraphyllidea the appearance of the uterus varies considerably in different families. In the Onchobothriidæ and Phyllobothriidæ it usually consists of a lobulated elongated sac. In a few species it is known that this sac definitely communicates with the exterior by means of a primary uterine pore situated on the ventral (flat) face of the segment; but in the vast majority of cases the eggs appear to be liberated by rupture of the wall of the segment, as in the Cyclophyllidea. It should be remembered, however, that in species of the above two families segments become detached from the chain before they are gravid, and in these instances the appearance of the gravid uterus is only known in a few species.

In the Proteocephalidæ the uterus resembles, in a general way, that found in the family Tæniidæ (Cyclophyllidea), in that it consists of a central stem with lateral branches; but in the former family the central stem is usually comparatively wide, as are also the lateral compound branches; moreover, in this family the uterus in each segment usually opens to the exterior by one or more pores.

In the order Trypanorhyncha the uterus is similar to that found in the two families Onchobothriidæ and Phyllobothriidæ (Tetraphyllidea).

In the monozootic cestodes the uterus in *Amphilina* is long and N-shaped, whilst in *Gyrocotyle* it is a closely convoluted tube lying in the mid-longitudinal axis and opening again near the anterior extremity.

Copulation.—Spermatozoa are transferred to the oviduct by means of the protrusile cirrus; the ova of one segment may be fertilized by the spermatozoa from the same segment or from another segment of the same chain; or, when many

strobilæ are present in the same host, by spermatozoa from another strobila. In the family Acoleidæ a vaginal pore is usually absent, and during copulation the cirrus apparently penetrates the tissue of the segment and the spermatozoa find their way to the ova.

Eggs.—The ovum is fertilized in the distal part of the oviduct (*oötype*), and it then receives the secretions from the vitelline gland and shell-gland when these are present: the whole is then enclosed in an egg-shell. In some cases the egg-shell appears to be developed from special vitelline cells, whilst in other cases it seems to be developed from cells derived from the segmenting ovum. In all cases the egg, when passed to the exterior, consists of a ball of cells (a morula) which contains typically six minute hooks, although in some cases ten or more may be present. This morula is called an *oncosphere* or a *hexacanth embryo*. It is usually enclosed in one or more envelopes or coverings. The one immediately surrounding the embryo, and secreted by the embryo, is called the *embryophore*. The outer covering is the *egg-shell*: between these two envelopes a third one is sometimes present, whilst in other cases the space between the two envelopes is filled with albuminous material or yolk.

In some genera of the family Anoplocephalidæ, the embryophore, instead of being a globular or oval sac, as in most other cestode eggs, is peculiar in that at one pole there are developed two prolongations, like the blades of a pair of scissors, and these may cross each other when fully developed. Such a structure is called a *pyriform apparatus*. In all eggs of the genus *Tænia* the egg-shell proper is a very delicate structure which is almost invariably ruptured and lost before the eggs (which, like most other cestode eggs, are passed in the fæces) reach the exterior. In such eggs the embryophore develops and becomes a very thick, radially striated structure, such a covering being necessary for the protection of the embryo.

Some eggs are colourless (*Hymenolepis*, *Dipylidium*, etc.), others are straw-coloured or light yellow (*Dibothriocephalus*), whilst in the case of all species of *Tænia* they are brownish when passed. They may be round, oval, or asymmetrical, and in some cases filaments are borne at one pole of the embryo; they vary in size from about 15 to 120 μ.

In some genera of Pseudophyllidea the eggs are operculated, *i. e.*, they bear a circular cap-like lid at one pole. This, which is called an *operculum*, fits very tightly, and in immature eggs it is often difficult to see. The operculum opens and allows the embryo to escape when the conditions are suitable.

Development and Life-history.—It should at once be remarked that, although many thousands of different species of tapeworms have been described, we are familiar with the life-

histories of comparatively very few (about 40). In all cases in which the life-history is known, further development of the egg takes place only after it has been swallowed by another host. It is quite possible, however, that, as knowledge increases, it may be found that many species do not require an intermediate host, and that in others two intermediate hosts are required.

It is a very remarkable and suggestive fact that, with one or two exceptions, all species included in the family Anoplocephalidæ occur in herbivorous and fruit-eating animals. In these cases it is difficult to believe that an intermediate host is necessary. It is of course possible that the larval form may develop in some small animal which is swallowed by the final host whilst eating grass, etc., but in the case of *Moniezia* all attempts to discover a larval cestode in insects, etc., which might be, and doubtless are, swallowed by sheep or cattle during feeding, have proved futile. This circumstance suggests the probability of the life-history being direct, and that in species of this genus infection with the adult worm takes place as a result of the eggs being swallowed. On the other hand, all attempts to infect lambs by feeding them with eggs of *Moniezia*, and also rabbits with eggs of *Cittotænia*, have failed.

As far as is known at present, all species of cestodes require at least two hosts to complete their development, except *Hymenolepis nana*. In the latter case the eggs, when swallowed by the proper host, penetrate the villi of the intestinal wall, develop into larvæ, drop into the lumen of the gut, to the wall of which they attach themselves, and then become adult. In this case the larval form and the adult worm develop in one individual as a result of the egg or eggs being swallowed.

In the Cyclophyllidea, Tetraphyllidea and Trypanorhyncha, as far as is known, two hosts only are required. The first, or intermediate, host usually becomes infected with the larva as a result of the pollution, with fæcal matter containing eggs, of the food or water taken by the animal. But from the egg only a larva can develop. The infection of the final host in which the adult worm occurs is brought about as a result of the final host devouring portions of the intermediate host infected with the larval form. In all cases the infection of both the intermediate host with larvæ and the final host with adult worms is brought about as a result of feeding in which the eggs or larvæ, always passive, are carried to their destination without any effort on their own part.

In all species of the Pseudophyllidea in which the life-history is known three hosts are required; the first larval host is a *Cyclops* or other crustacean, the second is a freshwater fish, and the third is the host in which the adult worm

occurs ; here again the connection existing between the various hosts is a food relationship.

Turning now to those species about which we have some knowledge, we find that in rare instances, e. g., *Hymenolepis nana* and *Tænia solium* *, further development may take place when the eggs are swallowed by the final host ; but in all other known cases, as we have noted above, a special intermediate host is necessary. This may be either a vertebrate or an invertebrate ; larvæ have been recorded from jelly-fish. In any case, when the egg is swallowed by a suitable host the embryo (oncosphere) escapes from the shell after this has been subjected to the influence of the digestive juices. The embryo is a small body, rarely measuring more than 20 μ, and usually much less ; it is amazingly active when once it has reached its proper host—a striking fact when one remembers that this is the only stage in its life-history when any degree of mobility is manifested. Such movements are necessitated by the fact that the naked and unprotected embryo must make its own way to the tissues of the host and finally encyst ; otherwise it would be voided in the fæces. With the assistance of its hooklets it bores its way through the intestinal wall and is carried to its normal habitat. This varies widely in the case of different species. When the intermediate host is a vertebrate, the larva usually enters a lymphatic or blood-vessel, and is presumably carried all over the body. The larvæ of the various cestodes exhibit remarkable selectivity for particular sites for their further development. In *Tænia saginata*, for example, the final larval stage is found only in the muscular system of the intermediate host, which in this case is the ox, and in the case of *Tænia multiceps* the larvæ only occur in the brain of the sheep. When the intermediate host is an arthropod, the final larval stage is found in the body-cavity.

We have already noted that, except in *Hymenolepis nana*, the final host can only become infected with the adult by swallowing the larval form. The latter consists essentially of the head, o· *scolex*, of the future worm, usually enclosed in one or more membranes. When this is swallowed, the membranes are digested and the larva is set free in the lumen of the digestive tract. By means of its suckers (and hooks, if they are present) it attaches itself to the wall of the intestine.

Growth.—The posterior portion of this head, or scolex, consists of proliferating tissue which, after the head becomes attached, is continually budding off new segments. At first these are very shallow—almost linear,—but as they become pushed further back, owing to other segments being produced, they gradually elongate and develop reproductive organs and,

* In this species the egg develops into a Cysticercus cellulosæ when swallowed accidentally by Man ; but the normal host of the larva is the pig.

finally, a uterus full of eggs. So that, whilst the segments immediately behind the head of any worm are small, and contain at most the rudiments of the genitalia, those in the middle of the worm contain fully developed genital organs, whilst the posterior segments are full of eggs.

Larval Forms.—Various types of larvæ occur, but they are reducible to two main forms, viz. :—

Solid Larvæ.—In this type the fertilized ovum continues uninterruptedly to segment, giving rise to a solid larva which, if globular, is called a plerocercus, and, if elongated, a plerocercoid ; the larval form of *Dibothriocephalus latus* is of the latter type.

Bladder Larvæ, such as those produced by the various species included in the genus *Tænia*. In these instances the egg when swallowed by the intermediate host is carried in the usual manner to the muscles or other tissues. On arrival, the cells in the centre of the segmenting embryo liquefy ; there is thus produced a small spherical body whose periphery is lined internally by proliferating cells, and in the centre of which there is a space containing liquid. Whenever this liquefaction of the centre of an embryo takes place, a bladder-worm of some sort is invariably produced. Three main types of bladders can be differentiated, viz. :—

A. A cysticercus such as C. bovis.—In this type there is one head. As the oncosphere enlarges, consisting as it does, primarily, of peripheral cells and a central cavity, a small invagination of the wall takes place, comparable to that which would be produced by pressing a finger into a soft india-rubber ball. At the bottom of this invagination the head of the adult worm develops, and this head can be evaginated. The result is that there is produced one bladder and one head. In the case of C. bovis and C. cellulosæ these bladders grow until they are the size of a small pea. Usually the head appears to be near one pole inside the cyst or bladder, and it can be seen with the naked eye, in fresh specimens, as a milky white patch about the size of a pin's head. When alive and fresh the head can be evaginated easily by light pressure between two slides.

The cysticerci, or larval forms, of the different species of the genus *Tænia* show considerable variation in form, and special names have been applied to them, as follows :—

(1) Strobilocercus Sambon, 1924.—In the larva of *T. tæniæformis* a chain of segments is budded off, in which, however, no genital organs are developed. On account of this larval peculiarity the adult worm has also been placed in a special genus or sub-genus to which the names *Hydatigera* Goeze, 1782, and *Reditænia* Sambon, 1924, have been applied.

(2) Dithyridium Rudolphi, 1819 (=Piestocystis Diesing, 1850).—This form is called a plerocercoid by many authors.

The latter term should be reserved for the larvæ of the Pseudophyllidea. It is elongated, and possesses a solid body without a caudal bladder. Anteriorly the scolex, which is provided with four suckers, but which is devoid of rostellum and hooks, is invaginated into the body in such a way that the head is turned inside out. It is probable that this larval form represents one or more species of the genus *Mesocestoides*.

(3) Cysticercoid Braun, 1883.—This is allied to a cysticercus, from which it differs in that the bladder is but slightly developed and is usually re-absorbed or cast off. Several modifications of the type occur, viz. :—

(*a*) Cryptocystis Villot, 1882.—This form occurs in the development of species of the genus *Dipylidium*. When the oncosphere liquefies, the cavity produced is relatively small. The larva elongates in such a way that it becomes literally divided up into a tail-like posterior part which contains the remains of the bladder and the embryonic hooks, and an anterior larger part which bears at its anterior extremity four suckers. The posterior part of the larva is cast off and atrophies, leaving only the solid anterior part, which may be considered as itself consisting of two parts, viz., an extreme anterior area on which suckers and hooks develop, and a posterior portion into which, eventually, the anterior part sinks. The scolex thus comes to be surrounded by a double wall, the whole simulating a cysticercus in appearance.

(*b*) Cercocystis Villot, 1882.—This type of larva occurs in the development of some species of the genus *Hymenolepis*. It resembles a cysticercus except that the tail is not cast off.

(*c*) Monocercus Villot, 1882.—This name is applied to those larvæ in which the scolex proper eventually lies free within the blastogene. It occurs in the development of some species of *Anomotænia*.

(*d*) Polycercus Villot, 1882.—This resembles a monocercus except that several scoleces are formed within a single blastogene. It is to all intents and purposes a cœnurus, from which it differs only in the following two points: (1) the scoleces become detached from the wall, and (2) they develop in a different manner.

There are other interesting modifications of the cysticercus type which cannot be considered in detail here.

B. Cœnurus Rudolphi, 1803.—Types :—Cœnurus cerebralis in the brain of sheep; Cœnurus serialis in the subcutaneous tissues of the rabbit; Cœnurus gaigeri in the nervous and subcutaneous tissues of the Indian goat.

This is a vesicle usually as large as a golf ball, and sometimes

larger. It consists of a single bladder and many heads. Each head is produced by an invagination of the wall in a manner precisely similar to what occurs in *C. bovis*. The cysts are easily differentiated from a hydatid by the following characters :—

The individual heads are large, always attached to the wall and easily seen with the naked eye, being milky white in colour : they occur in conspicuous clusters here and there on the cyst wall, the rest of which is free from scoleces, whereas in a hydatid cyst the brood capsules (which contain scoleces) are small and difficult to see with the naked eye : the wall of the cyst is homogeneous and does not show the milky-white patches so typical of a cœnurus.

C. Echinococcus Rudolphi, 1801.—The hydatid cyst in the liver (and other organs) of cattle, horses, sheep, etc., and occasionally in man. The adult worms are *Tænia echinococcus* and closely related species, found in the dog, cat, fox, etc. This is the largest of all tapeworm cysts : it attains the size of a child's head. In its final form it is full of liquid, in which many bladders and many heads occur.

Whereas in cysticercus and cœnurus each invagination gives rise to one head only, which never becomes detached from the cyst-wall, in echinococcus each invagination produces either (1) a brood capsule or (2) a daughter cyst, both of which become detached from the wall of the cyst.

In the case of a brood capsule the cavity of each of the original invaginations becomes studded with secondary invaginations, so that there is produced a ball of heads which separates from the wall of the cyst and comes to lie in the liquid filling the cyst. This ball of scoleces is always small, much smaller than that of a single head in cœnurus and cysticercus, and it rarely measures more than 1 mm. Having separated from the wall of the cyst, the parenchymatous tissue holding the heads together disintegrates, and thus the scoleces become detached from each other within the original cyst. A hydatid cyst contains an albuminous or serous fluid from which, when allowed to stand, a sediment settles at the bottom. This sediment is often called "sand." It consists of enormous numbers of extremely small, solitary scoleces and a large number of brood capsules in process of disintegration into separated scoleces. As, however, the internal wall of the cyst is in a continuous state of proliferation, the process of disintegration is never completed.

In cattle a very heavy infection with hydatid cysts is common, and in such cases the individual cysts are smaller than usual and very frequently sterile or barren—that is, no "sand" is produced inside the cyst.

A few of the original invaginations may, instead of ceasing to grow when they attain a size of about 1 mm., grow very large, frequently as large as a small hen's egg, and they are then known as daughter cysts. They, too, become detached from the wall of the parent cyst, and resemble the parent in every particular, except that they are smaller. Frequently, when a hydatid cyst is punctured these daughter cysts float out like small balloons.

The daughter cysts are of two kinds, viz., endogenous when they develop inside the parent cyst, and exogenous when they grow outside the wall of the parent cyst.

Occasionally, in the liver of an animal, the parent cysts grow under considerable pressure. In such cases the cysts, instead of being globular, grow by tunnelling a way in the tissues, and portions of these channels may become isolated. This type of hydatid is referred to as Echinococcus multilocularis.

Each of the above types of bladder worm, *i.e.*, cysticercus, cœnurus, and echinococcus, is produced from a single egg.

In cysticercus one bladder and one head (the infective organism) results, so that one egg eventually produces again only one adult worm. In cœnurus and echinococcus, however, large numbers of heads or scoleces are produced, so that in both these instances one egg, having passed through the intermediate host, eventually gives rise to a very large number of adult worms. Where one egg gives rise to more than one adult, asexual multiplication (alternation of generations or heterogeny) has taken place.

In cysticercus no alternation of generations, or asexual reproduction, occurs, because, as pointed out above, one egg produces finally only one adult worm.

Diagnosis of Cestode Infections.

This is often a difficult matter; in infected animals the fæces usually contain eggs, and these can be found when a smear of fæcal matter is examined microscopically. In light infections it may be necessary to concentrate the eggs from a small quantity of fæces. To find eggs in the case of herbivorous animals like the horse it is usually necessary to make the fæces liquid by the addition of water. A portion is then taken and strained through a fine sieve, or through butter cloth. The eggs in the filtrate are then concentrated in the usual manner.

Many of the larger worms such as *T. solium*, *T. saginata*, *Dibothriocephalus latus*, *Moniezia* spp., and *Dipylidium caninum*, etc., pass segments in the fæces which can be easily identified.

Relation of Host to Parasite and Parasite to Host.

It is true that we are familiar with the results of parasitism in man and in those domestic animals of importance to man; but we know very little regarding the effects produced by cestode parasites in birds and other lower animals, since these are unimportant economically.

In mammals an eosinophilia, varying in intensity up to 60 or 70 per cent., sometimes occurs in an individual infected with either cestodes, trematodes, or nematodes.

The parasites may be so numerous, or so large, as to obliterate the lumen of the intestine. It appears certain, however, that the symptoms, when these are present, produced by cestode parasites are due in a large measure to the excretory products called toxins, which are elaborated by these parasites and absorbed by the host.

In man the presence of a cestode worm usually produces discomfort, and not infrequently gives rise to nervous and other symptoms. There is no part of the human body from which Cysticercus cellulosæ has not been recorded. Should this larva occur in muscle, connective tissue, etc., its presence is more or less unimportant, but if it occurs in the eye or brain, as it frequently does, the results are serious.

Lambs infected with *Moniezia* do not thrive, and are usually anæmic. On the other hand, dogs are found apparently quite healthy, but nevertheless harbouring one or more parasites.

The larval form of *Tænia tæniæformis* (Cysticercus fasciolaris) may occur so abundantly in the liver and body-cavity of rats and mice as to prove fatal, and Sambon associates this condition with cancerous growths frequently found along with the parasites.

The writer recently examined a duck which had died, and found several hundreds of tapeworms in its intestine; the conclusion that these parasites were responsible for the death of the host was irresistible.

Davainea friedbergeri gives rise to purulent desquamative intestinal catarrh, with general anæmia, in pheasants.

Many hundreds of crows (*Corvus* spp.) in Calcutta have been examined, and all, without exception, were found more or less heavily infected, in spite of which they appeared healthy.

Amongst reptiles the writer has never observed any sign of disease, even when large numbers of cestode parasites have been present in the intestine, and the same can be said about elasmobranch fishes. Amongst marine teleostean fishes, however, diseased conditions are much more common. Cystic forms frequently occur, not only in the body-cavity, but in the musculature, especially in the lumbar muscles. When in the latter position the cysts, which often attain the size of 10 mm.,

atrophy and disintegrate; the result is that inflammatory reactions on the part of the host take place, necrosis occurs, and pus forms producing an ulcer often 2 inches in diameter.

Very few observations have been made relating to the effect on the parasites produced by different hosts.

Amongst elasmobranch fishes the relation of the host to the parasite, and *vice versa*, is one of considerable importance. The adult parasites almost invariably occur in the spiral valve. When the head of the parasite becomes attached, its position is at first marked by a prominent hæmorrhagic patch. Later on the hæmorrhage ceases, and the position of the head of the worm is much less distinct. Calcification of the area then commences, and results in the production of large calcareous nodules with which the spiral valves of old infected fish are studded. As a result of this calcification, the head of the parasite becomes subjected to pressure and breaks up, later on itself becoming calcified. The worm thus becomes detached from the wall of the intestine of the host and is passed to the exterior. Hooks of *Acanthobothrium ijimai* and *Acanthobothrium coronatum* have been found by the writer in the calcareous nodules which occur in the spiral valve of various species of *Dasybatus* and *Carcharias*, and there can be no doubt that the pathological reactions of the host have the effect of limiting the infestation.

Orientation of a Cestode.

The anterior end of the worm is here considered as being that extremity which carries the head, and the posterior extremity that furthest removed from the head. The ventral surface of the worm is that surface nearest the ovary.

In the Cyclophyllidea, Tetraphyllidea, and Trypanorhyncha with few exceptions, and in some Pseudophyllidea, the ventral surface can only be determined by locating the position of the ovary in transverse sections. When a uterine pore is present it is usually situated ventrally, as in most species of the order Pseudophyllidea (except the family Ptychobothriidæ) and in the family Proteocephalidæ. In these cases the ventral surface can be determined without sectioning.

In certain species of the genus *Avitellina* it is often extremely difficult, if not impossible, in the absence of a scolex, to determine which is the anterior and which is the posterior part of a fragment of a worm several inches in length. This circumstance is due to the fact that external segmentation is not evident, although the genital organs indicate that the segments are extremely shallow, often not more than 50 μ in length.

Abnormalities.

Abnormalities and malformations are extremely common. Fenestration of the strobila has been described, and worms with two heads, sterile segments interpolated between mature or gravid segments, imperfect segmentation, fusion of segments, entire or partial duplication of the genitalia, etc., are by no means rare.

Species of *Tænia* are sometimes found in which, instead of there being two rows of hooks, the rows are indistinct, and the hooks appear to be irregularly arranged on the rostellum. Larval nematode parasites have been found in the longitudinal excretory vessels, and the writer has frequently encountered what appeared to be clusters of parasitic organisms in the parenchyma of the strobila. On one or two occasions he has obtained worms in which calcification had commenced.

Anoplocephala perfoliata is a parasite of the horse. In a large number of specimens of this worm taken from a zebra it was found that, although the male and female genital organs developed in the normal manner, no eggs were produced—the posterior half of the worm, the segments of which should have contained a gravid uterus, were sterile.

Position of Cestode within its Host.

Adult cestodes are, with few exceptions, parasitic in the intestine of vertebrates. *Stilesia hepatica* occurs, however, in the liver and bile ducts of sheep, and a species of *Nematotænia* has been recorded from the pericardial sac of a frog. Tetraphyllidea are rarely found except in relation with the spiral valve of elasmobranch fishes. Baer has recently reported species of *Hymenolepis* from an insect. Larval forms of cestodes have been recorded from practically all classes of animals, from jelly-fish upwards, and in nearly every type of tissue or cavity.

Fixation and Preservation of Cestodes.

Except in large animals such as cattle, horses, etc., the intestine should be removed from the pylorus to the anus, and freed from mesenteric tissues until it can be laid out in the form of a more or less straight tube. Where eggs or gravid segments are to be examined, portions of the fæcal matter from the lower part of the rectum should be removed and preserved as indicated below. The intestinal wall is now split open longitudinally from one end to the other, placed in a basin, and washed in running tap-water for one or two hours. If this is not possible, then it may be placed in fresh water, changed three or four times, until the internal intestinal wall is perfectly clean. It is advisable in the latter case to stir the tissue at frequent intervals; when the water is changed, care

should be taken to remove any segments, or worms, from the debris. If the intestine is too large to place in a basin it is best to cut it up into suitable lengths and examine each part separately. It is found that in fresh water the worms, after a time, loosen their hold on the tissue and become free in the water. This is very important, because when a head is present the identification of the parasite is a comparatively simple matter. If, however, the worm possesses no head, the identification of the species is often impossible. The worms should never be forcibly pulled off from their attachments, because in so doing the heads are almost certain to be left behind.

Normal salt solution should not be used for washing the worms. Meggitt (1924) states that cold water also should not be used for washing them, but in the writer's experience excellent results have been obtained by the method detailed above.

After having become free, the worms should be removed to another basin and washed in running water for an hour or two, or, failing that, in frequent changes of water. They should then be preserved in 3 per cent. formalin. If the worms are small they can be placed directly in the 3 per cent. formalin. In some instances the parasites are so minute that they can hardly be seen with the naked eye, as, for instance, in *Amœbotænia sphenoides*, *Tænia echinococcus*, and *Davainea proglottina*, etc. To find these worms it is often necessary to examine with a hand-lens the sediment obtained after washing. In some cases, as for instance *Tænia echinococcus*, the worms are embedded in the mucosa, and have for the most part to be dissected out. This should be done under a binocular microscope by means of two fine triangular needles mounted in holders. In the case of large worms, such as species of *Tænia*, it is advisable to lay them out straight between two panes of glass and run the preserving fluid on to them whilst in this position. This has the effect of preserving them in a straight condition, but great care should be taken that they are not squeezed, but merely held in position, otherwise the genital organs, muscular system, etc., will become displaced, and sections and whole mounts will convey a wrong impression as to the disposition of these organs. After remaining between two panes of glass for a few hours the worms can then be transferred to a bottle and preserved in the usual way in 3 per cent. formalin. With *Tænia* and *Moniezia*, it is necessary to change the formalin after a few days. In all cases a few drops of glycerine should be added to the formalin so that should the liquid evaporate sufficient glycerine will be left behind to keep the worms moist. If the parasite becomes dry it is useless to attempt an identification.

It should be noted that the preservation of cestode worms in alcohol is not advised, as the writer's experience has shown

that in this fluid they become brittle and brown, whilst in formalin they remain soft and supple.

Each bottle should contain a label giving the

PLACE.
DATE.
HOST.
WHERE FOUND IN HOST (liver, intestine, skin, etc.).
COLLECTOR'S NAME.

Labels should be written on thick paper in Indian ink, allowing the ink to dry before placing them inside the bottles.

Cestode larvæ should also be preserved in 3 per cent. formalin.

Other fluids than formalin can be used for fixing cestode worms, but in the writer's experience they do not give better results. Amongst them may be mentioned the following :—

(1) *Bouin's Fluid.*
Saturated aqueous solution of picric acid, 75 parts.
Formalin (*i. e.*, 40 per cent. formaldehyde solution), 25 parts.
Glacial acetic acid, 5 parts.

(2) *Zenker's Fluid.*
Corrosive sublimate, 5 grm.
Glacial acetic acid, 5 c.c.
Potassium bichromate, 2 grm.
Distilled water, 100 c.c.

If either of the above fluids is employed, the worms should be allowed to remain in the solution for at least 24 hours. Baylis (1922) suggests the following procedure :—Each worm is picked up " by the end remote from the scolex, and, allowing it to hang down, when its own weight will usually cause it to stretch sufficiently, it may then be dipped quickly several times in a jar of the fixing fluid."

In dealing with minute forms such as those detailed above, it is desirable that the worms should be pipetted in and out of the fixative.

After fixing in either of the above fluids, it is necessary to wash the parasites in running water for a protracted period, otherwise they cannot satisfactorily be stained. After washing, they can be preserved in 3 per cent. formalin to which has been added a few drops of glycerine.

Staining.

The choice of a stain is a matter of individual taste. The writer has found the following two to be most suitable, and of these the first has yielded the better resulte :—

(1) *Acetic Acid Alum-carmine.*—This stain is prepared as

follows :—An excess of carmine is boiled for about 15 minutes in a saturated watery solution of potash alum ; 10 per cent. of glacial acetic acid is added ; allow to stand for about a week and filter. Before staining, the worms should be placed in running water for several hours in order to dissolve out any trace of the preserving fluid. Good results cannot be obtained unless this washing process is carried out properly. After washing they are placed in the stain, which is used diluted in the proportion of one part to from 8 to 10 parts of water. In the case of small worms staining is complete in less than an hour, but with large worms it is desirable to leave them in the stain over night. They should then be removed and placed for a few minutes in running water ; they are then transferred to 50 per cent. alcohol for about 30 minutes and then to 70 per cent. acid alcohol * for a similar length of time. This medium dissolves out the stain from the cortex but leaves it in the genital organs, unless it is allowed to act for too long a period.

As large worms have a tendency to twist when placed in alcohol, the writer, when differentiating with acid alcohol, places them between two pieces of glass, taking care that the pressure is just sufficient to keep the worms straight, but not to squeeze them. The acid alcohol is pipetted between the two pieces of glass. The worms are allowed to remain in this position for about two hours, and are then transferred to a vessel also containing 70 per cent. acid alcohol until differentiation is complete. They are then placed in absolute alcohol until dehydrated, and finally in clove oil until transparent. They are then ready for mounting in Canada balsam.

(2) *Delafield's Hæmatoxylin* is prepared as follows :—To 400 c.c. of saturated solution of ammonia-alum (ammonia-alum dissolves in about 11 parts of water) add 4 grm. hæmatoxylin crystals dissolved in 25 c.c. of 90 per cent. alcohol. Leave exposed to the light and air in an unstoppered bottle for three to four days. Filter and add 100 c.c. of glycerine and 100 c.c. of methyl alcohol. Allow the solution to stand until the colour is dark, then filter and keep in a tightly stoppered bottle.

It is well to allow it to ripen for at least two months before using. The stain is used very dilute, a few drops being added to distilled water until a somewhat faint purple colour is obtained.

The procedure is the same as with acetic acid alum-carmine.

* 100 c.c. of 70 per cent. alcohol to which has been added 5 drops of hydrochloric acid.

Use of Carbolic Acid.

Worms placed in pure carbolic acid become transparent, and this medium is therefore useful when a hurried examination is desirable or when a permanent mount is not necessary. It is a particularly useful medium in which to examine scoleces, eggs, or gravid segments. The procedure is as follows :—

Whether the parasite is fresh or preserved, it may be dropped directly into pure carbolic acid. Small worms like *Davainea proglottina* will become clear in about 5 minutes; larger ones, such as *Dipylidium caninum*, take about 20 minutes. The time occupied in making any of the larger worms transparent is greatly reduced if they are first placed for a few minutes in 70 per cent. alcohol. In the case of minute parasites this is not necessary. After examination, the worms can be transferred to the fluid from which they were removed, and this process can be repeated often without any ill effects, except that such a specimen cannot subsequently be stained.

At low temperatures carbolic acid crystallizes with great rapidity. This can be obviated by using a mixture consisting of 95 parts of carbolic acid and 5 parts of absolute alcohol.

Occasionally, in pure carbolic acid, objects become so transparent on the slide that they are almost invisible. The degree of opacity required can be obtained by running a small quantity of absolute alcohol along the margin of the cover-slip.

If a permanent preparation of the object is desired, the cover-slip should be ringed with a mixture containing equal parts of hard wax and Canada balsam which has been melted ; it should be applied with a small glass rod. If too much carbolic acid has been used in mounting, and some of it adheres to the margin of the cover-slip, either at the time of mounting or subsequently, the ringing will not be permanent, and consequently the specimen will dry up.

Preservation of Fæces.

Except in the case of the common parasites found in man and domestic animals, the gravid segments and mature eggs of most species of cestodes are not well known. The reason is that helminthologists, up to the present, have contented themselves with collecting and preserving adult forms, and no attention has been paid to the mature eggs and gravid segments which are frequently contained in the fæces of the host. It is therefore very desirable that in all animals (birds, fishes, etc.) found to be infested with tapeworms the whole or a portion of the fæces from the rectum should be preserved,

because such fæcal matter will probably contain gravid segments and mature eggs from the worm or worms found parasitic in the intestine.

In the case of small animals like birds, lizards, elasmobranch fishes, etc., the whole of the rectal contents should be preserved, but in the larger ones such as crocodiles, cattle, etc., the rectal contents are so voluminous that only a portion can be kept. The procedure is as follows :—

1. A suitable quantity of fæcal matter is placed in a container; if hard and formed, it should be made of the consistency of porridge by the addition of water.

2. Formalin, 5 per cent., equal to 10 times the volume of fæcal matter taken, is brought to the boiling-point and poured slowly over the fæcal matter, stirring the while.

3. The mixture is allowed to stand until sedimentation is complete ; the supernatant fluid is then poured off carefully and a fresh quantity of cold 5 per cent. formalin is added.

Examination of Fæces.

(1) *Small Animals.*

(*a*) *Fresh Fæces.*—A small drop of water is placed in the centre of a slide : by means of a platinum loop fixed into a glass holder 6 or 7 inches in length, a small quantity of fæces is picked up and emulsified in the drop of water on the slide; after covering, the preparation is ready for microscopic examination.

(*b*) *Preserved Fæces.*—After shaking up the preserved fæces, a small drop is removed by means of a pipette, and transferred to a glass slide under a cover-slip.

In both the above cases a low-power objective should be employed, and it is always necessary that the light should be cut off by means of the iris diaphragm until the best definition is obtained.

(2) *Large Animals.*

In cases where the quantity of fæcal matter in the rectum is considerable, gravid segments, when present, can be found much more easily if a small portion of the fæces is diluted with water and examined, either on a slate table or in a large black photographic developing dish. This procedure can be followed until the whole of the fæcal matter has been examined. Under these conditions cestode segments show up white against the black background, and are thus easily seen. It is advisable, however, when using a black developing dish, that the water

should not be more than a quarter of an inch deep, otherwise the segments cannot be seen through the turbid water.

When the fæces are to be examined for eggs, it is desirable to make the whole or part of the stool liquid by the addition of water. The mixture should then be passed through a fine sieve, some of the filtrate centrifuged, and a portion of the deposit examined microscopically under a cover-slip. In light infections it may be necessary to concentrate the eggs in the filtrate.

CESTODA.

A class of the phylum Platyhelminthes, characterized as follows :—

The body (strobila) is flat, tape-like, does not bear cilia, and is unsegmented or consists of a number of segments ; in a few species external segmentation is indistinct. At the anterior extremity the head (scolex) is usually armed with either suckers or hooks or both. An alimentary canal is entirely absent. The parenchyma usually contains scattered calcareous corpuscles. Except in the new family Dioicocestidæ male and female genital organs are developed in each segment. The egg contains a morula with six (sometimes more) hooklets. With very few exceptions all adult species are parasitic in the intestine. So far as is known at least two hosts are required to complete the life-history, except in very few species. The larval form, which consists essentially of the head of the future worm, occurs in both vertebrates and invertebrates.

After dividing the class into the two orders Cestodaria and Eucestoda (=Cestoda, s. str.), six superfamilies of Eucestoda are recognized : three of these, viz. Tænioidea, Tetrarhynchoidea, and Dibothriocephaloidea are identical with the Cyclophyllidea, Trypanorhyncha, and Pseudophyllidea respectively. The families Lecanicephalidæ and Proteocephalidæ have hitherto been included with the families Phyllobothriidæ and Onchobothriidæ in the order Tetraphyllidea. As the head in species of the former two families is very different from that in those of the latter two, it has been found desirable to include the Phyllobothriidæ and Onchobothriidæ in one superfamily and to create two new superfamilies for the Lecanicephalidæ and Proteocephalidæ, which differ from each other in the form of the head and the appearance of the uterus.

The class is accordingly divided as follows :—

Order I. Cestodaria Monticelli, 1892.
Monozootic Cestodes of authors.

Family 1. Amphilinidæ Claus, 1879.
,, 2. Caryophyllæidæ Müller, 1787.
,, 3. Gyrocotylidæ Benham, 1901.

Order II. Eucestoda, nov.
Polyzootic Cestodes of authors.

Superfamily I. Dibothriocephaloidea Stiles, 1906.
Synonyms :—Pseudophyllidea Carus, 1863.
Bothriocephaloidea Braun, 1903.

Family 1. Dibothriocephalidæ Lühe, 1902.
„ 2. Triænophoridæ Nybelin, 1920.
„ 3. Ptychobothriidæ Lühe, 1902.
„ 4. Amphicotylidæ Nybelin, 1920.
„ 5. Echinophallidæ Schumacher, 1914.

Superfamily II. Tetrarhynchoidea, nov.
Synonym :—Trypanorhyncha Diesing, 1863.

Family 1. Tetrarhynchidæ Cobbold, 1864.
„ 2. Cœnomorphidæ Lühe, 1910.
„ 3. Haplobothriidæ Meggitt, 1924.

Superfamily III. Phyllobothrioidea, nov.
Synonym :—Tetraphyllidea Carus, 1863.

Family 1. Phyllobothriidæ Braun, 1900.
„ 2. Onchobothriidæ Braun, 1900.

Superfamily IV. Lecanicephaloidea, nov.
Family Lecanicephalidæ Braun, 1900.

Superfamily V. Proteocephaloidea, nov.
Family Proteocephalidæ La Rue, 1911.

Superfamily VI. Tænioidea Zwicke, 1841.
Synonym :—Cyclophyllidea Braun, 1900.

Family 1. Tæniidæ Ludwig, 1886.
„ 2. Anoplocephalidæ Cholodkowsky, 1902.
„ 3. Davaineidæ Fuhrmann, 1907.
„ 4. Hymenolepididæ Railliet & Henry, 1909.
„ 5. Dilepididæ Railliet & Henry, 1909.
„ 6. Mesocestoididæ Fuhrmann, 1907.
„ 7. Nematotæniidæ Lühe, 1910.
„ 8. Amabiliidæ Fuhrmann, 1908.
„ 9. Acoleidæ Ransom, 1909.
„ 10. Tetrabothriidæ Linton, 1891.
„ 11. Dioicocestidæ, nov.

Genera of uncertain Systematic Position.

1. Echinobothrium van Beneden, 1890.
2. Discocephalum Linton, 1890.
3. Diagonobothrium Shipley & Hornell, 1906.
4. Pillersia Southwell, 1927.

Key to Orders.

Monozootic cestodes, *i. e.*, worms composed of a single segment	I. **Cestodaria.**
Polyzootic cestodes, *i. e.*, worms composed of many segments	II. **Eucestoda.**

Key to Superfamilies.

1. Head bears two sucking grooves which may be variously modified, or with a terminal fixation organ..............	**Dibothriocephaloidea.**
Head does not bear two sucking grooves ..	2.
2. Head bears four protrusile proboscides ..	**Tetrarhynchoidea.**
Head does not bear four protrusile proboscides	3.
3. Head composed of four ear-like outgrowths or lappets, variously modified .	**Phyllobothrioidea.**
Head not composed of four ear-like outgrowths or lappets..................	4.
4. Head bears four suckers; acini of vitelline glands condensed into a single mass..........	**Tænioidea.**
Head bears four suckers; acini of vitelline glands scattered and not condensed into a single mass	5.
5. Head composed of two parts except in *Cephalobothrium*, where one part is replaced by a sucker................	**Lecanicephaloidea.**
Head not composed of two parts, but simple	**Proteocephaloidea.**

Order I. CESTODARIA Monticelli, 1892.

Pallas in 1781 described a worm from a bream (*Abramis* sp.) under the name *Tænia laticeps*. Müller in 1787 erected the genus *Caryophyllæus*, and described a worm belonging thereto which appears to be the *Tænia laticeps* of Pallas. It is clear that it belongs to that group of worms which are now called monozootic cestodes.

Diesing (1850) erected the genus *Gyrocotyle* for other monozootic cestodes found in the intestine of certain fishes, particularly *Chimæra* spp.

In 1858 Wagener discovered other worms in the cœlom and intestine of marine fishes, and placed them in a new genus which he named *Amphilina*.

Leuckart (1878) found monozootic cestodes in the body-cavity of annelid worms.

Braun (1883) erected the family Amphilinidæ to contain the genera *Amphilina* Wagener, 1858, and *Amphiptyches* Grube & Wagener, 1852 (=*Gyrocotyle* Diesing, 1850). His definition of the family was: "oval or leaf-shaped worms, without a distinct head, but with a single small acetabulum at one end."

Monticelli in 1902 placed together in a class which he called Cestodaria all those cestodes which contain a single set of genital organs, and in which, consequently, the body is not segmented.

Plehn (1905) described two worms from the blood of cyprinoid fishes for which she erected the genus *Sanguinicola*, and which she referred to a group which she named Rhynchostomida. Odhner (1911) rightly referred these worms to the Trematoda.

Cooper (1918) in his monograph on the Pseudophyllidea did not include the family Caryophyllæidæ, being apparently of the opinion that it did not belong to this order.

Nybelin (1922) erected the family Cyathocephalidæ, which he divided into two subfamilies, namely, Cyathocephalinæ Lühe, 1899, and Caryophyllinæ Nybelin, 1922. In the first subfamily he placed the genus *Cyathocephalus* Kessler, 1868, and in the second he included the genera *Caryophyllæus* Müller, 1787, and *Archigetes* Leuckart, 1878.

Woodland (1923) divided the monozootic cestodes as follows :—

Order I. Amphilinidea.
Family Amphilinidæ.

Order II. Paralinidea.
Family 1. Caryophyllæidæ (with three genera only, viz., *Caryophyllæus*, *Archigetes*, and *Wenyonia*).

2. Gyrocotylidæ.

He pointed out that the latter family was closely related to the Bothriocephalidæ.

Fuhrmann and Baer (1925) do not, however, accept Woodland's classification, which they regard as a regression, pointing out that Lönnberg, in 1897, showed that the Caryophyllidæ are secondarily monozootic, whereas the Gyrocotylidæ are primarily monozootic.

There appears to be an element of doubt as to whether Lönnberg's contention is correct, and in any case the species are monozootic.

Poche (1926) classified the group as follows :—

Subclass Amphilinoinei Poche, 1926.

Order (*a*) Amphilinidea Poche, 1922.

Family I. Amphilinidæ Claus, 1879.

Subfamily 1. Amphilininæ Poche, 1926 (containing the genus *Schizochærus* Poche, 1922).

Type-species :—*Schizochærus liguloideus* (Diesing, 1850) Poche, 1922.

Synonym :—*Amphilina liguloidea* (Diesing, 1850) Monticelli, 1892.

Subfamily 2. Gephyrolininæ Poche, 1926.

Genus *Gephyrolina* Poche, 1926.

Type-species :—*Gephyrolina paragonopora* (Woodland, 1923).

Subfamily 3. Gigantolininæ Poche, 1922.

Type-genus :—*Gigantolina* Poche, 1922.

Type-species :—*Gigantolina magna* (Southwell, 1915).

Order (*b*) Gyrocotylidea Poche, 1926.

Family Gyrocotylidæ Benham, 1901.

Type-genus :—*Gyrocotyle* Diesing, 1850.

Hunter (1929) reinstated Leuckart's family Caryophyllæidæ and placed it in the order Pseudophyllidea.

It is thus clear that opinions are divided regarding the systematic position of those genera included in the family Caryophyllæidæ Leuckart (quoted by Claus, 1885). In this volume all the monozootic cestodes are referred to the order Cestodaria Monticelli, 1892, which is regarded as containing three families only, viz., Caryophyllæidæ, Amphilinidæ, and Gyrocotylidæ.

Order Cestodaria Monticelli, 1892.

Worms varying in size up to 30 cm. in length and 2 cm. in breadth. They are unsegmented, and contain a single set of genital organs. Parasitic in the intestine or body-cavity of fishes and annelid worms.

These forms are in some respects intermediate between the Trematoda and the Cestoda; they resemble the former in appearance, but differ from them in the absence of an alimentary canal. Morphologically they are like cestodes, but differ from the majority of species in this class in never containing more than a single set of genital organs.

Key to Families.

Uterus not N-shaped, but consisting of a coiled median tube	I. **Caryophyllæidæ**, [p. 43.
Uterus very long, with three limbs like the letter N, two of which lie laterally, one on each side	II. **Amphilinidæ**, [p. 46.

No species of the family Gyrocotylidæ have been recorded from India.

Family I. CARYOPHYLLÆIDÆ Leuckart (quoted by Claus, 1885).

Body usually elongated, and oval in cross-section, occasionally leaf-like; calcareous corpuscles and cuticular spines or hooks absent. Testes situated in a single field, always anteriorly to the uterus. The uterine and vaginal apertures are situated close together, ventrally, a little in front of the middle of the worm. Uterus a coiled tube extending about half the length of the worm in the median longitudinal axis. Parasitic in the intestine of bony fishes.

Type-genus :—*Caryophyllæus* Müller, 1787.

Genus 1. CARYOPHYLLÆUS Müller, 1787.

Anterior extremity of strobila without bothria, and functioning as a fixation organ. Excretory system with a well-developed terminal bladder. Longitudinal muscles in two layers, one of which lies external to the nuclear layer of the subcuticula, the other separating the medullary from the cortical parenchyma. Cirrus sac and common vaginal and uterine pore open close together in a shallow genital cloaca. Vas deferens very coiled ; cirrus sac large ; receptaculum seminis conspicuous, separated from the oviduct. Ovary posterior and H-shaped, situated in the medullary parenchyma. Vitellaria in the medullary parenchyma, sometimes placed partly behind the ovary. Coils of the uterus posterior to cirrus sac. Adults in bony fishes. Larval stages (*procercoid*) in annelids.

Type-species :—*Caryophyllæus laticeps* (Pallas, 1781).

Only one species of this family has been recorded from India.

Caryophyllæus indicus Moghe, 1925. (Fig. 3.)

From *Clarias batrachus* *, Nagpur, C.P., India. Moghe.

The worm measures 2·5 cm. in length and has a maximum breadth of 4·4 mm. The scolex is short, bluntly rounded, much narrower than the body, and measures 3 mm. in length and 1·23 mm. in breadth. It is marked off from the rest of the body by a small neck-like constriction. The body tapers posteriorly, and shows no trace of internal or external segmentation. The genital apertures are situated one-seventh the length of the body from the posterior extremity ; the aperture of the cirrus sac is separate ; the uterus and vagina open by a common aperture.

The testes are scattered among the acini of the vitellaria : they occupy nearly two-thirds the length of the body. The vas deferens is a loosely convoluted tube running anteriorly in the median axis of the body. The cirrus sac is large and bell-shaped, its longitudinal axis lying parallel to the longitudinal axis of the body.

The ovary is irregular in shape, and is situated posteriorly between the genital openings and the posterior end of the body. The vagina is a narrow tube running in the median longitudinal axis ; anteriorly it dilates, and the uterus opens into the dilatation. Posterior to the ovary the vagina receives the small duct from the transverse vitelline sac. The vitellaria occupy the greater part of the body between the genital

* The names given to the elasmobranch fish hosts in the succeeding parts of this work have kindly been determined by Mr. Norman of the British Museum, and are in accordance with the International Rules of Nomenclature.

openings and the head; they are most abundant laterally. The uterus arises as a thin-walled duct, situated posteriorly to the transverse vitelline sac. It runs to the posterior end of the body, then turns and, running anteriorly, forms several conspicuous thick-walled loops on each side of the body posterior to the genital apertures, one loop on each side being at the level of the genital apertures. Near its junction with the vagina it is distinctly narrow and ciliated. The uterine eggs measure 80 by 40 μ.

Woodland (1926) points out that this is the first species of the genus to be recorded from a siluroid fish. He suspects

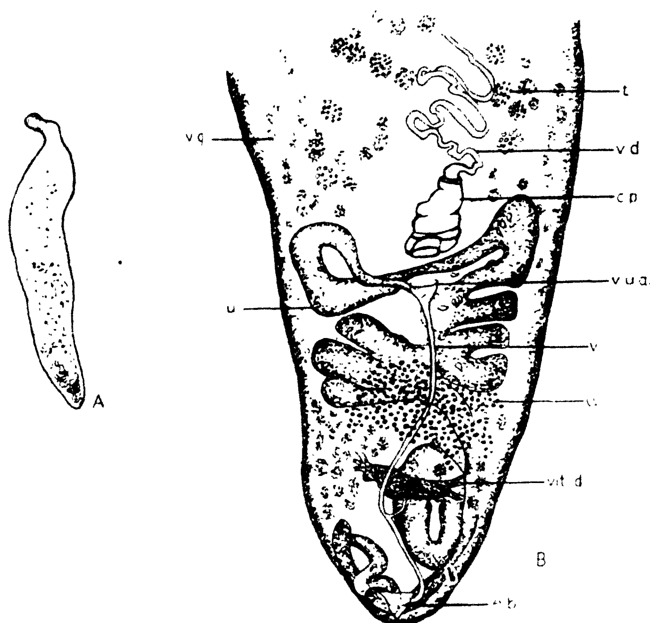


Fig. 3. *Caryophyllæus indicus.* A, entire worm, × 1·7; B, posterior extremity, magnification unknown. (After Moghe, in 'Parasitology.')

that the bodies figured as post-ovarian vitellaria are really ovarian follicles, and that the species belongs to the genus *Lytocestus* (found in silurids), the characters of which are as follows:—

Genus II. **LYTOCESTUS** Cohn, 1908.

Scolex insufficiently known. Musculature consists of two longitudinal layers (and one transverse layer), the outer layer being situated internal to the nuclear layer of the subcuticula,

and not external to it as in the genus *Caryophyllæus*. Genital pores surficial, posterior; uterine pore absent. Genitalia in the posterior half of the segment. Testes numerous, filling the entire medullary parenchyma anterior to the cirrus sac. Ovary posterior to genital pore, its follicles extending into the cortex. Vitellaria encircling the worm and situated in the cortical parenchyma, not extending behind the ovary. Wall of the uterus glandular: the uterus coils between the wings of the ovary, the receptaculum seminis, and the genital pore.

Parasitic in the intestine of Siluridæ and Mormyridæ.

Family II. AMPHILINIDÆ Claus, 1879.

Body flattened, usually elongated and tape-like; calcareous corpuscles present, but cuticular spines and hooks absent. Testes in two strips, one along each lateral margin, parallel to the limbs of the uterus. The uterine and vaginal pores are situated at opposite ends of the body, the former being anterior and the latter posterior. Uterus very long with three limbs, like the letter N, two of which lie laterally, one on each side of the worm. Parasitic in the body-cavity of fishes.

Type-genus:—*Amphilina* Wagener, 1858.

Genus **AMPHILINA** Wagener, 1858.

Body flat, unsegmented, and usually very elongated; suckers absent. Anteriorly a number of very large unicellular glands open, sometimes on a small papilla. Skin unarmed; female genital pore posterior, a little in front of the male pore. Uterine pore at the anterior extremity of the body. The excretory system consists of anastomosing vessels with pore posterior. Testes very numerous, in two narrow lateral bands extending almost the length of the worm; vitelline glands also in two lateral bands external to the testes. Cirrus sac absent. Ovary posterior; uterus very long, N-shaped. Eggs containing an embryo which bears ten hooklets.

Type-species:—*Amphilina foliacea* (Rudolphi, 1819) Wagener, 1858.

(1) **Amphilina magna** Southwell, 1915. (**Figs. 4 & 5.**)

Synonym:—*Gigantolina magna* (Southwell, 1915) Poche, 1921.

From *Diagramma crassispinum*, **Pearl Banks, Ceylon. South-well.**

When alive, the worm attains a maximum length of 38 cm. and a breadth of nearly 1 cm., with a thickness of about 1·5 mm. When preserved they shrink very considerably. They are flat with parallel margins, milky white in colour, broadly rounded at one extremity, and terminating at the other

Fig. 4.

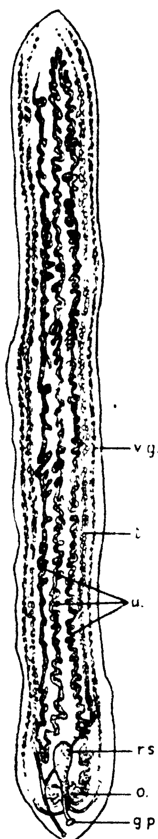
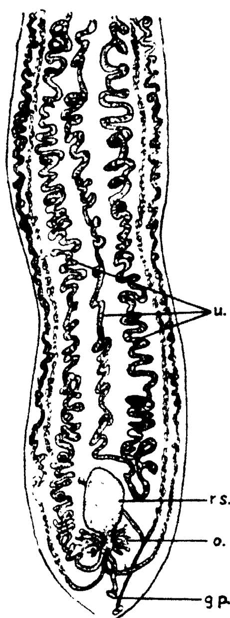


Fig. 5.



Amphilina magna.

Fig. 4.—Entire worm, × about ¼. (After Southwell.)
Fig. 5.—Posterior extremity, × about ½. (Modified, after Southwell.)

extremity in an acute point. The uterine pore is situated ventrally near the anterior extremity ; the vagina also opens ventrally near the posterior extremity, a little in front of the vas deferens. The skin does not bear spines, but is marked

by a fine honeycomb-like sculpture. A number of large unicellular glands (frontal glands) open at the anterior extremity.

Male Genitalia.—The testes number over 2000. They are arranged in two narrow, symmetrical, lateral, longitudinal bands situated just median to the vitellaria and extending from the anterior to the posterior extremity. Here and there these bands are overlapped dorsally and ventrally by a coil of the uterus. The breadth of each testicular band is about 600 μ; vasa efferentia traverse each testicular band antero-posteriorly; the posterior extremity of each band is continuous with a collecting duct, the two uniting together on the left side into a vas deferens which runs posteriorly and opens at the posterior extremity of the worm, dilating a little in its course into a seminal vesicle. Just to the right of the male genital pore traces of the persisting embryonic hooks may be found.

Female Genitalia.—The ovary has a breadth of about 3·5 to 5 mm., and is situated posteriorly: it is bilobed, butterfly-shaped, and consists of two wings, each wing being composed of a collection of tubules arranged transversely. From the posterior extremity of the ovary the uterus arises and also a small duct which receives the secretions from the shell and vitelline glands. It discharges into a vagina which pursues a direct posterior course, opening behind a little in front of the male genital pore, and close to a rather prominent muscular ring. The vagina continues in front of the ovary as a receptaculum seminis: this is a comparatively large structure measuring 7 mm. in length and 3·5 mm. in breadth. The shell gland is a somewhat globular organ situated between the two wings of the ovary.

The vitelline glands consist of two narrow bands situated laterally, externally to the uterus and testes, and extending almost the whole length of the body. From the posterior extremity of each lateral band a duct arises; the two ducts turn anteriorly and unite near the muscular ring; the common duct runs forward to open with the shell gland into the oviduct.

The uterus arises close to the shell gland and runs in close coils along one margin of the worm almost to the anterior extremity (first ascending branch), and turns backwards and runs posteriorly to a point a little in front of the ovary (descending branch), it then turns again (second ascending branch) and, running anteriorly, opens by a small ventral pore close to the anterior extremity of the worm.

The egg measures from 100 to about 150 μ in diameter: no filaments have hitherto been observed.

(2) **Amphilina paragonopora** Woodland, 1923. (Fig. 6.)

Synonym:—*Gephyrolina paragonopora* (Woodland, 1925) Poche, 1926.

From (1) *Macrones aor* and *M. seenghala*, Rivers Ganges and Jumna, United Provinces, and the Punjab, India. Woodland. (2) *Bagarius yarrelli* (*Pimelodes bagarius*), Allahabad, India. Verma.

The largest specimens, when alive, measured 25 cm. in length, 5 mm. in maximum breadth, and had a thickness of

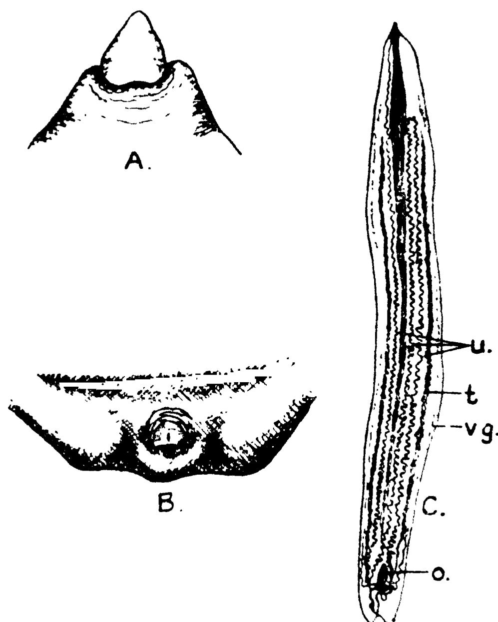


Fig. 6.—*Amphilina paragonopora.* A, anterior extremity; B, posterior extremity, showing openings of the vagina and ductus ejaculatorius; C, entire worm, × about 4½. (After Woodland, in the Q. J. M. S.)

about 1 mm. When preserved they contracted to 17 cm. in length. Small specimens measuring 10 mm. in length and 1 mm. in breadth are common. The parasites are ribbon-like, and vary in colour from creamy-white to orange-yellow, usually being distinctly yellowish. A scolex is absent. The anterior extremity, which is either rounded or pointed, bears a papilla, on which numerous large unicellular glands open. The posterior extremity of the worm terminates in a well-

marked semicircular depression, in the centre of which there is a contractile papilla on which are situated the excretory and vaginal pores and the opening of the ductus ejaculatorius.

The general internal anatomy of the species resembles that of *Amphilina magna* Southwell, 1915.

Order II. EUCESTODA, nov.

POLYZOOTIC CESTODES.

Superfamily I. DIBOTHRIOCEPHALOIDEA Stiles, 1906.

Synonyms :—Pseudophyllidea Carus, 1863.
Bothriocephaloidea Braun, 1903.

Rudolphi (1809) divided the cestodes into two orders. The first order, Cystica, contained the three genera *Cysticercus*, *Cœnurus*, and *Echinococcus*. The other order, Cestoidea, included six genera only, namely, *Scolex*, *Caryophyllæus*, *Ligula*, *Tricuspidaria*, *Bothriocephalus*, and *Tœnia*.

In 1819 he defined these genera; his description of the genus *Bothriocephalus* was as follows: "*Corpus elongatum depressum articulatum, caput subtetragonum bothriis duobus vel quatuor oppositis.*"

He divided the genus into two main groups, namely, (1) those in which the head was unarmed (*inermes*), and (2) those in which it was armed (*armati*). The first group he sub divided again into two, viz., those with two bothria and those with four bothria. All the species in his group *armati* had four bothria, and were subdivided again into two sections; the first section contained the species *B. coronatus*, *B. uncinatus*, *B. verticillatus* (later included in the order Tetraphyllidea); the second section contained those worms armed with proboscides, namely, *B. corollatus* and *B. paleaceus* (later included in the order Trypanorhyncha).

Dujardin (1845) recognized four orders of cestodes, viz. :—

(1) Rhynchobothriens (Tetrarhynchids).
(2) Cestoides or Tænioides, including the genera *Tœnia*, *Bothriocephalus*, *Schistocephalus*, *Triænophorus*, *Bothridium*, *Bothrimonus*, and *Ligula*.
(3) Scolecines, including *Caryophyllæus* and some larval forms, and
(4) Cystiques—all bladder worms.

Van Beneden (1850) only mentioned two genera of bothriocephalids, viz., *Bothriocephalus* and *Tricuspidaria*, and these he included in his division Pseudophylles.

Diesing's classification (1850 and 1864) was extremely complicated, introducing as it did a large number of mere names which have since fallen into synonymy.

Carus (1863) divided the cestodes into five families, namely, Caryophyllidea, Tetraphyllidea, Diphyllidea, Pseudophyllidea, and Tæniadea. In the family Pseudophyllidea he included four genera, namely, *Ligula* Bloch, *Triænophorus* Rudolphi, *Schistocephalus* Creplin, and *Bothriocephalus* Bremser (*sic*).

Lühe in 1899 published an admirable classification of the order; this was adopted by Braun in 1900, and it has only been slightly modified during recent years.

Cooper in 1918 issued an excellent account of the Pseudophyllidea of the North American fishes.

Nybelin in 1922 published his classic work on this order. His classification differs from that proposed by Lühe (1902) only in the following point. Nybelin retains the family name Dibothriocephalidæ Lühe, 1902, instead of the later name, Diphyllobothriidæ used by Lühe in 1910 for the same family.

There appears to be some doubt as to which name has priority, because Lühe, who established the genus *Dibothriocephalus* in 1899, citing *latus* as the type-species, afterwards made this genus a synonym of *Diphyllobothrium* Cobbold, 1858. The anatomy, however, of the type-species of the latter genus is not known, and, until the position of the pores in this species has been determined, it is doubtful whether the genera *Dibothriocephalus* Lühe, 1899, and *Diphyllobothrium* Cobbold, 1858, are synonymous.

Poche (1926) divided the class Cestoidea into two subclasses, one of which included the order Bothriocephalidea Diesing, 1850 (=Pseudophyllidea Carus, 1863), and contained the following.—

Subclass Tænioinei Poche, 1926.

Order 1. Bothriocephalidea Diesing, 1850.

Tribe 1. Caryophyllæoidæ Poche, 1926.

Family 1. Cyathocephalidæ Nybelin, 1920 (with five genera).

Family 2. Caryophyllæidæ Claus, 1879 (with nine genera).

Tribe 2. Diphyllobothrioidæ Poche, 1926.

Family 1. Diphyllobothriidæ Lühe, 1910. Including the genus *Diphyllobothrium* Cobbold, 1858. ? = *Dibothriocephalus* Lühe, 1899.

Family 2. Luheellidæ Baer, 1924.
Genus *Luheella* Baer, 1924.

Tribe 3. Bothriocephaloidæ Poche, 1926.

Family 1. Bothriocephalidæ Blanchard, 1849 (with five genera).

Tribe 4. Triænophoroidæ Poche, 1926.

Family 1. Triænophoridæ Blanchard, 1849.
,, 2. Amphicotylidæ Ariola, 1899.
,, 3. Echinophallidæ Schumacher, 1914.

Tribe 5. Tetrabothrioidæ Poche, 1926 = Tetrabothria Diesing, 1850.

Family 4. Tetrabothridæ Fuhrmann, 1908.

Pintner (1928) divided the class Cestoidea into two orders: (1) Monozootic and (2) Polyzootic forms. All pseudophyllidean cestodes are placed by him in a single family, namely, Bothriocephalidæ, all species of which are polyzootic.

Superfamily Dibothriocephaloidea Stiles, 1906.

Synonyms:—Pseudophyllidea Carus, 1863.
Bothriocephaloidea Braun, 1903.

Strobila segmented. Scolex with two shallow grooves (*bothria*), which by fusion of their margins may assume various forms, or they may be replaced by a pseudoscolex or by a terminal sucker. Accessory suckers may be present. The head may be either armed or unarmed. External segmentation often incomplete or absent. Segments in the same stage of development. Genital pores marginal or surficial (*i. e.*, on the flat side). A single or double set of genitalia in each segment. Vitelline follicles usually in the cortex, scattered, not condensed into a single gland. Testes situated either in the cortex or medulla. Uterus persistent, often in the form of a rosette, sometimes a large sac distinct from the uterine duct. Three genital pores present; uterine pore almost always surficial. Openings of vagina and vas deferens may be close to that of the uterus, or on the opposite flat side, or along the lateral margin. Eggs, which may be operculated or not, are passed whilst the segments are still attached to the strobila. Oncosphere frequently with a ciliated covering (*coracidium*). Development, where known, into a procercoid in the body-cavity of Entomostraca succeeded by a plerocercoid in teleosts. Adults in mammals, birds, reptiles, and fishes.

Considerable difficulty has been experienced with reference to this superfamily. Cobbold in 1858 erected the genus *Diphyllobothrium*, the type-species being *Diphyllobothrium*

stemmacephalum Cobbold, 1858, a worm obtained from a dolphin. In 1879 he created the family Diphyllobothridæ, which Lühe emended in 1910 to Diphyllobothriidæ. The latter author had in 1899 erected the genus *Dibothriocephalus* (type-species: *Dibothriocephalus latus* Linnæus, 1758), which in 1902 he placed in his family Dibothriocephalidæ.

Later on Lühe made his genus *Dibothriocephalus* a synonym of *Diphyllobothrium* Cobbold, 1858. It is not known whether the three genital pores in the type-species of the latter genus are all on one surface or not. If they are, then Lühe was correct, but if not, then the two genera are not synonymous. Unfortunately, the point cannot be settled until the parasite from the dolphin has been re-studied. As the type-species of Lühe's genus, viz., *Dibothriocephalus latus* (Linnæus, 1758), is so well known, it appeared desirable to accept his genus, and the superfamily is named accordingly.

The superfamily is divided into five families, viz., Dibothriocephalidæ, Triænophoridæ, Ptychobothriidæ, Amphicotylidæ, and Echinophallidæ, only three of which are represented in India.

Key to Families.

1. Genital pores marginal	**Triænophoridæ**, p. 64.
Genital pores surficial	2.
2. Genital pores and uterine pore on the same surface	**Dibothriocephalidæ**, [p. 53.
Genital pores and uterine pore on opposite surfaces	**Ptychobothriidæ**, p. 66.

Family I. DIBOTHRIOCEPHALIDÆ Lühe, 1902.

Synonyms: Diphyllobothridæ Cobbold, 1879.
Diphyllobothriidæ Lühe, 1910.

Head armed or unarmed, bothria shallow, one dorsal, one ventral, or their free margins may fuse to form a tube open at both ends, or there may be a terminal unpaired sucker. A single set, rarely a double set, of genitalia in each segment. Genital pores surficial. Male and female pores open close to, and a little in front of, the uterine pore. Vas deferens with an external seminal vesicle. Cirrus unarmed. Receptaculum seminis sharply separated from the oviduct. Uterus a long coiled tube, often in the form of a rosette. Eggs operculated. Adults in mammals, birds, and reptiles. First larval stage (procercoid) in Entomostraca. Second larval stage (plerocercoid) in teleosts.

Type-genus :—*Dibothriocephalus* Lühe, 1899.

Subfamily I. DIBOTHRIOCEPHALINÆ Lühe, 1899.

Scolex elongated, clearly separated from the strobila. Bothria variable in form. External segmentation distinct. A single or double set of genitalia in each segment. Eggs operculated. Adults in mammals, birds, and reptiles. Larval stages in Crustacea and fishes.

Type-genus :—*Dibothriocephalus* Lühe, 1899.

Genus I. **DIBOTHRIOCEPHALUS** Lühe, 1899.

Synonym :—*Diphyllobothrium* Cobbold, 1858.

Bothridia elongated and well developed. A single or double set of genitalia in each segment. Testes and vitellaria lateral, in some cases almost reaching the median line, but they may fuse anteriorly or posteriorly. Uterus a coiled tube situated anteriorly, often in the form of a rosette. Adults in mammals and birds. First larval stage (*procercoid*) in copepods ; second larval stage (*plerocercoid*) in teleosts ; or larval stage a solid proliferating unsegmented form, without bothria, in musculature of mammals.

Type-species :—*Dibothriocephalus latus* (Linnæus, 1758) Lühe, 1899.

(1) **Dibothriocephalus felis** (Creplin, 1825). (Fig. 7.)

Synonyms : *Bothriocephalus maculatus* Leuckart, 1848.
Dibothrium decipiens Diesing, 1850.

From (1) *Felis tigris* and *F. pardus*, Zoological Gardens, Calcutta. Southwell. (2) *F. nebulosa* and the domestic cat, Calcutta. Chandler.

The worm was first described by Creplin in 1825 from two small specimens measuring 4·5 mm. and 6·6 mm. respectively, obtained from the cat. Leuckart's species *Bothriocephalus maculatus* was obtained from *F. pardus* and measured 16 cm. in length.

Böhm (1921) considers that Molin's species *Dibothrium sulcatum* is identical with *Bothriocephalus felis* Leuckart, 1848. According to Ariola (1900) *D. sulcatum* differs from all other related species in having the bothria lateral instead of dorsal and ventral.

The worms measure up to 25 cm. in length, and have a maximum breadth of 8·8 mm. The proglottides are all broader than long, the genital pores are situated on the flat ventral surface (surficial), the opening of the vas deferens is close to the anterior border of the proglottis, and the vaginal pore is

immediately posterior to it. The uterine pore is posterior and somewhat lateral to the vaginal pore. The latero-posterior margin of each proglottis overlaps the anterior lateral margin of the succeeding one.

The scolex is unarmed, and bears two shallow bothridia, one situated dorsally and one ventrally.

The testes are numerous, situated in the medulla, and extend over the dorsal surface, except in the median line. In ordinary stained specimens they are indistinguishable from the

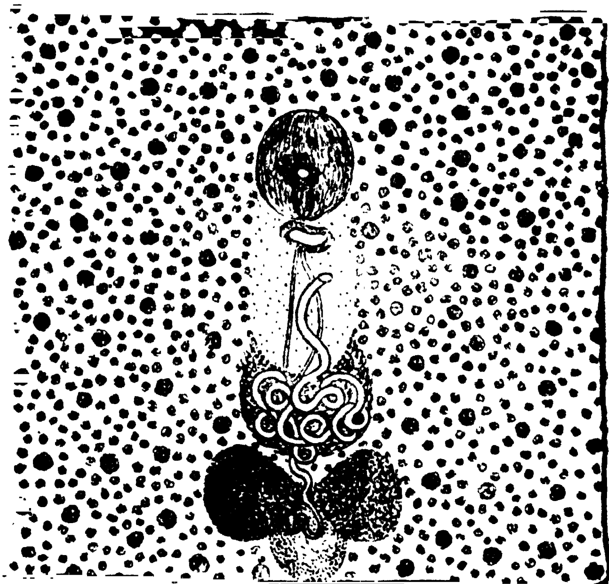


Fig. 7.—*Dibothriocephalus felis.* Mature segment, × 50. (After Southwell.)

acini of the vitelline glands, which have a similar distribution, except that they are situated in the cortex.

The vas deferens arises posteriorly and runs almost in the median line to the pore. The ovary is bilobed and situated posteriorly.

The vagina is a straight tube running directly in the median line from the ovary to the pore. The two transverse vitelline ducts, one from each side and situated posteriorly, unite together in the middle line and open into the oötype.

The uterus assumes the form of a rosette, and in fresh specimens appears as a brown patch in the middle of the proglottis.

The eggs are operculated and measure about 60 by 30 μ.

(2) **Dibothriocephalus reptans** (Diesing, 1850).

Synonym:—*Sparganum reptans* Diesing, 1850.

From *Tropidonotus* sp., Burma. Meggitt.

The larval form is parasitic in reptiles and occurs usually in the connective tissue between the dorsal muscles, especially along the vertebral column and between the skin and dorsal musculature. It has been recorded from various species of amphibia, birds, and mammals. Meggitt states that all records of this parasite other than those from reptiles should be regarded with suspicion, as it is probable that several have been confused under one name.

The plerocercoid is a slender ribbon-like form with an anterior globular swelling; it varies in length from 2 mm. to 10 cm., and is capable of asexual reproduction by fragmentation, but not by proliferation. It has no definite scolex or bothria. The terminal invagination referred to by various writers bears no trace of the structure of a sucker, and is the result of contraction due to fixation: it is, however, probable that the anterior extremity functions as a sucker. External and internal segmentation is usually absent, but occasionally in very long forms it may be represented by a few posterior transverse striations. The internal anatomy shows nothing of note except the absence of "nutritive bodies" described by Ijima (1905) for S. proliferum and Meggitt (1924) for Sparganum sp. It is not known whether procercoids occur in Entomostraca or not.

The adult form has been obtained experimentally in the dog. The true host is probably a carnivore or avian scavenger. It measures 1 metre in length, and has a breadth of 9 mm. Segmentation is complete. The scolex is elongated, and measures 800 by 40 μ; it bears two long shallow bothria. The neck is long. All segments are broader than long. The musculature is weak, consisting of a narrow and feeble layer of longitudinal muscle. Transverse muscles are apparently absent.

The excretory vessels are indistinct, consisting of from four to eight longitudinal trunks on each side of the proglottis, connected by an extensive and complicated capillary system. The genital pores are surficial, and are all on the same surface of the proglottis; the male pore is central, in the anterior sixth of the segment; the vaginal pore lies posterior to it and slightly lateral, and the uterine pore is more posterior and central. The cirrus sac extends halfway to the opposite surface, the external vesicula seminalis nearly reaching the

aporal cortical parenchyma. The testes number from 144 to 220, and are situated in two separate lateral bands, slightly converging anteriorly. The ovary is bilobed, reticulate, and the shell gland is a large structure lying at the posterior margin of the proglottis. The vitelline glands are lateral, converging and meeting anteriorly, leave a free central space one-twelfth to one-seventh the width of the segment.

The egg measures from 53 to 59 μ by 36 to 40 μ and is operculated. It is immature when passed, but develops when it rests in water.

(3) **Dibothriocephalus ranarum** (Gastaldi, 1854).

Synonym:—*Ligula ranarum* Gastaldi, 1854.

Larval forms from *Rana tigrina*, Burma. Bhalerao.

The larval form occurs in the wall of the stomach of the frog *Rana tigrina*; it measures 8·5 cm. in length and 1·1 mm. in breadth. At the anterior extremity there is a small terminal bothrium, like a sucker in appearance, but histologically not differentiated from the surrounding parenchyma. The degree of external segmentation varies: it is sometimes ill-defined or limited, especially in young specimens, whilst in older specimens it may be well defined and almost complete. Transverse fission (asexual reproduction) occurs. The musculature is weak, and varies in different parts of the body. In some parts of the worm definite longitudinal muscle bundles and dorso-ventral fibres occur. Transverse muscles are apparently absent. In transverse sections four main longitudinal excretory vessels can be seen in the same transverse straight line across the proglottis, linked with each other by a complex capillary anastomosis. Only the rudiments of the genital organs are present, and " nutritive bodies " are apparently absent.

The adult worm has been obtained experimentally in the dog. It measures 113 cm. in length and 5 mm. in breadth. The scolex measures 1·4 to 1·7 mm. in length by 370 to 410 μ in breadth. All the proglottides are either broader than long or square. The male genital pore is median, and lies almost at the anterior margin of the proglottis. Slightly behind, and a little lateral to it, is the vaginal pore. The testes are in two lateral groups, 100 to 110 in each group, and not joined together by an anterior band. The uterus has from three to five coils on each side. The eggs measure 58 to 67 μ by 34 to 36 μ.

Joyeux and Baer (1927) state that *D. reptans* and *D. ranarum* are identical; they call the worm " *D. ranarum* according to the laws of nomenclature." They found procercoids of this species in *Cyclops fuscus* Jurine, plerocercoids in *Tropidonotus natrix* Linn., and adult worms in cats and dogs. If Joyeux and Baer's contention is correct, it would appear that the specific name *reptans* has priority.

Faust, in an abstract of a paper contributed for the fourth annual meeting of the American Society of Parasitologists held in December 1928 ('Journal of Parasitology,' vol. xv, No. 2, December 1928), concluded that four well defined species of *Dibothriocephalus* develop as adults in cats or dogs, namely, *D. mansoni*, *D. decipiens*, *D. ranarum*, and *D. erinacei*; the larval forms of these species (Spargana) develop in a variety of vertebrate hosts such as frogs, snakes, and mammals. Faust thus agrees with Joyeux.

Species inquirendæ.

Dibothriocephalus sp.

Moghe (1926) mentions the occurrence of an undetermined species in the leopard cat (*Felis bengalensis*).

Diphyllobothrium spp.

Under the name *Bothriocephalus* sp., Southwell (1922) recorded a species of the genus from a black leopard (*Felis melas*). The worm measured 2 cm. in length and had a maximum breadth of 1·2 mm. The specimen was quite immature. He also recorded a single worm of this genus from the Himalayan palm civet (*Paradoxurus grayi*). The worm measured 10 cm. in length and had a maximum breadth of 6·7 mm. As the head was absent the species could not be determined.

Genus II. BOTHRIDIUM Blainville, 1824.

Synonym:—*Solenophorus* Crepin, 1839.

Scolex with two tubular bothridia which open anteriorly and posteriorly by pores provided with sphincter muscles. Vitelline glands between inner and outer longitudinal muscles, sometimes intermingling with the latter. Uterus consists of a uterine duct and a uterine sac, which latter is composed of two large cavities connected by a narrow duct.

Type-species:—*Bothridium pithonis* Blainville, 1824.

Bothridium pithonis Blainville, 1824. (Fig. 8.)

Synonyms:—*Prodicœlia ditrema* Lebl., 1836.
Bothridium laticeps Duvern, 1833.
Solenophorus megalocephalus Creplin, 1839.
Solenophorus grandis Creplin, 1839.

From *Python reticularis*, Goalundo, Bengal; *P. molurus*, Nepal Terai and Ceylon; and *Felis tigris*, Onchagaon, Naini Tal, India. Southwell. (It appears probable that the tiger had been feeding on a python.)

The worm measures up to 50 cm. in length and has a maximum breadth of 6 mm. It is composed of an immense number of very shallow segments: the largest segment has a breadth of 6 mm. and a length of 700 μ. A few of the posterior segments are narrower and longer, measuring 2·5 mm. in breadth and 1·5 mm. in length. The mid-dorsal and ventral surfaces of the worm are marked by a longitudinal line which can be seen with the naked eye. In the large specimens the head measures 6 mm. in length and 4 mm. in breadth. The bothria are tubular, each with a small, slit-like aperture anteriorly and a smaller



Fig. 8.—*Bothridium pithonis.* Head. × 6.
(After Southwell.)

one posteriorly. They are situated dorsally and ventrally, *i. e.*, at right angles to the flat side of the worm.

The cuticle is very thick and the subcuticular cells are very large. The longitudinal musculature consists of about twelve fasciæ distributed round the proglottis. The transverse muscles are delicate and send out fibres which ramify in the longitudinal muscles. The dorso-ventral bundles are small. There are four principal excretory vessels, two on each side of the segment; the lateral nerves lie external to these vessels. The testes number from 170 to 180, and are situated in two lateral fields, one on each side of the median line posteriorly to the cirrus sac. The latter organ varies in shape, measuring 250 μ in length by 175 to 345 μ in breadth. The genital pores are surficial. The vagina opens immediately behind the cirrus

pouch into a common deep atrium situated at the junction of the first and second thirds of the proglottis. The uterine pore is situated at the junction of the middle and posterior thirds of the proglottis. The genital pores are irregularly alternate. The vagina runs directly posterior to the cirrus sac. The receptaculum seminis is large and thick-walled. The ovary is V-shaped, the apex being directed dorsally; it is surrounded by the testes, which approach the median line. A shell gland is present. The uterus lies in two loops on each side of the median line; the last loop is dilated. The egg measures 65 to 70 μ by 45 μ and is operculated.

SPECIES INQUIRENDA.

Bothridium sp.

Moghe (1926) records *Solenophorus* sp. from the python (rock snake) but he does not describe the worm.

Genus III. **DUTHIERSIA** Perrier, 1873.

Scolex triangular, the apex being directed posteriorly. Bothridia funnel-shaped. Vitelline glands lateral and external to the longitudinal muscles. Vaginal sphincter present. Uterus coiled, but not definitely in the form of a rosette. Adults in *Varanus*.

Type-species :—*Duthiersia fimbriata* (Diesing, 1850).

Duthiersia fimbriata (Diesing, 1850), Mont. & Crety, 1891. (Figs. 9 & 10.)

Synonyms :—*Duthiersia expansa* Perrier, 1873.
Duthiersia elegans Perrier, 1873.

From *Varanus bengalensis*, *V. exacanthematicus*, and *Varanus* sp., Ceylon, Bengal, and Punjab. Southwell.

The worms usually measure about 7 cm. in length and have a maximum breadth of 2 mm. They attain, however, a much greater size than this, and may measure 20 cm. or more in length by 3 mm. in breadth, with a thickness of 1·5 mm. The broadest part of the worm is near the middle. The largest proglottides have a breadth of about 2 mm. and a length of about 300 μ; a few of the more posterior segments are longer and narrower than the rest, having a length of 500 μ and a breadth of 1 mm. The posterior extremity of the worm is frequently very narrow. The scolex has a length of about 3 mm. and a breadth of 3 mm. It is roughly triangular in shape, with the rounded apex pointing anteriorly. It is composed of two bothria, one dorsal and one ventral, united in the middle line, with their lateral margins scalloped and overhanging a rather shallow sucker.

There is no neck. The excretory system consists of a large ventral vessel and a small dorsal vessel on each side, situated in the medulla, a considerable distance from the lateral margins,

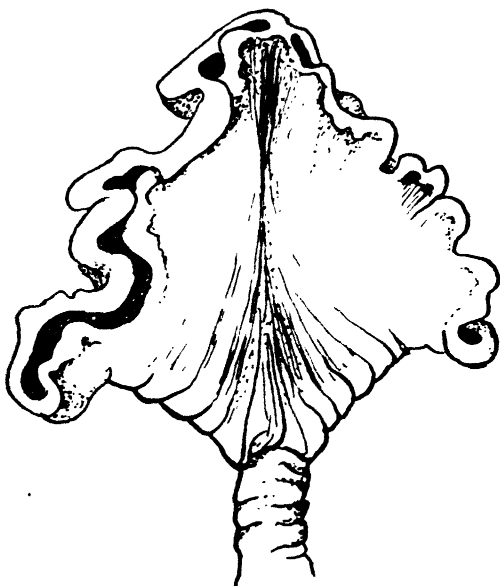


Fig. 9.—*Duthiersia fimbriata.* Head. × 20.
(After Southwell.)

anastomosing extensively, so that in transverse sections three vessels, and sometimes more, are to be seen on each side ; the third longitudinal vessel is often situated external to the

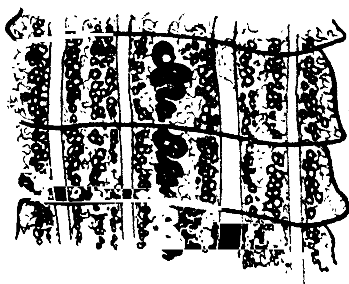


Fig. 10.—*Duthiersia fimbriata.* Segments, × 10.
(After Southwell.)

lateral nervous system. There is a single longitudinal nerve running along each lateral margin of the worm close to the ventral excretory vessel, and situated in the medulla. The

longitudinal muscles are not segregated into definite fasciæ, but consist of a very large number of fibres situated close together encircling the segment, and to all intents and purposes dividing the parenchyma into cortex and medulla. Circular and dorso-ventral fibres are very scanty. The testes are small, not numerous, and are situated in the medullary parenchyma, extending laterally to the excretory vessels. The vas deferens opens ventrally near to the anterior margin of the proglottis. The ovary is bilobed and situated posteriorly; it frequently presents a granular appearance. The vagina runs forward almost in a straight line, opening just posterior to the vas deferens. The vitelline glands are numerous, strongly developed, and situated in the cortex, practically enveloping the proglottis. The uterus assumes the form of a rosette, frequently showing about five loops, but these loops are often ill-defined. The uterine egg measures about 60 by 40 μ and is operculated.

Group **SPARGANUM** Diesing, 1855.

This name is applied to larval forms (plerocercoids) of the family Dibothriocephalidæ, the adults of which are not known. Segmentation absent or indistinct. Bothria sometimes indistinct.

SPARGANUM sp. I.

Meggitt (1924) records a Sparganum from the mesentery and body-cavity of the mongoose (*Herpestes albopunctatus* [? *auropunctatus*]). The earliest stages consist of a spherical solid larva containing numerous calcareous corpuscles surrounded by a cyst-wall consisting of several concentric, transparent, and apparently gelatinous layers, sometimes tinged with red. The large forms are elongated, broad, flattened, with a slight invagination at one end but no trace of suckers or segmentation. The larva proliferates like Sparganum proliferum Ijima, 1905. No definite organs of any kind are to be seen even in section, but "nutritive bodies" are numerous.

SPARGANUM sp. II.

Meggitt (1926) reports the presence of a Sparganum in *Dichoceros bicornis*, but he does not describe it.

Subfamily II. LIGULINÆ Monticelli & Crety, 1891.

Scolex small, triangular, unarmed, and not clearly separated from the strobila. Bothria small and rudimentary. External segmentation often indistinct. Genital pores ventral. Adults in mammals and birds. Larvæ in fishes.

Type-genus :—*Ligula* Bloch, 1782.

Genus LIGULA Bloch, 1782.

Bothria and external segmentation absent in larva, but both develop simultaneously with the genitalia in the final host. Segmentation in adult limited to anterior portion of strobila, and does not correspond with the genital organs. Adults in birds.

Type-species :—*Ligula intestinalis* (Linnæus, 1758).

Ligula intestinalis (Linnæus, 1758). (Fig. 11.)

Synonymy extensive.

From *Labeo calbasu*, *Labeo rohita*, and *Nemachilus rupicola*, India. Southwell.

Both the larvæ and adult worms vary in length from 10

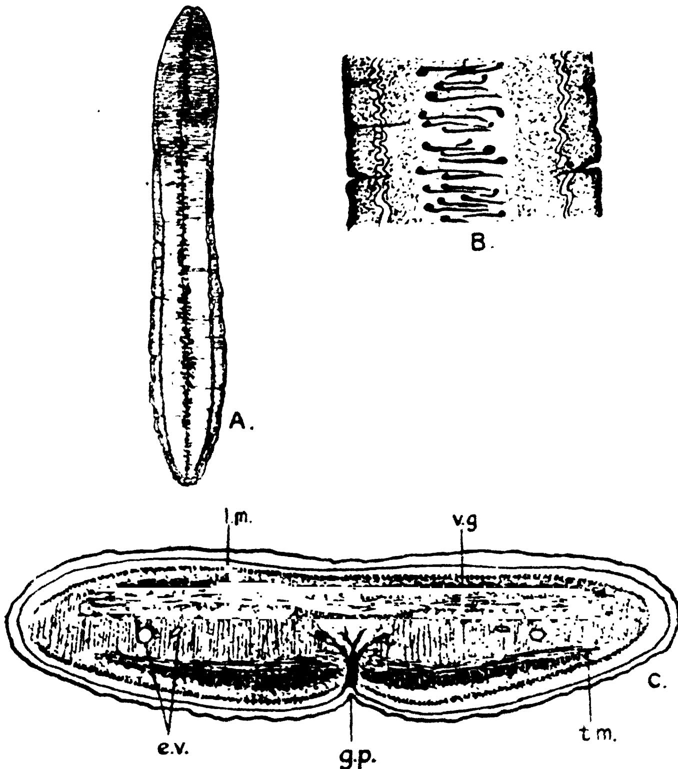


Fig. 11.—*Ligula intestinalis*. A, entire worm, × 2 ; B, horizontal section, × 7 ; C, transverse section, × 18. (After Southwell.)

to 40 cm., sometimes attaining 1 m. The breadth varies from 5 mm. to 1·5 cm. The larvæ occur in the body-cavity of various Cyprinoid fishes and adult worms in various

fish-eating birds. The adults differ but little from the larval form.

Only larval forms have been recorded from India.

SPECIES INQUIRENDA.

Moghe (1926) recorded *Ligula* sp. from *Rasbora daniconius*, India, but he did not describe it.

Family II. TRIÆNOPHORIDÆ Nybelin, 1920.

Scolex armed or unarmed, with two shallow bothria and an anterior, flattened, disc-like termination. In one genus, viz., ***Fistulicola***, a pseudoscolex is present. Genital pores marginal (not surficial), alternating. Receptaculum seminis and vesicula seminalis absent. Uterus a coiled duct, its pore being ventral. Eggs operculated. Adults in fishes and turtles.

Type-genus :—*Triænophorus* Rudolphi, 1793.

Four genera are usually referred to this family, namely :—

- *Triænophorus* Rud., 1793, in which external segmentation of the strobila is absent.
- *Ancistrocephalus* Lühe, 1879, in which the strobila is segmented externally and the scolex is armed.
- *Fistulicola* Lühe, 1899, in which the strobila is segmented externally, head unarmed and testes for the most part situated internal to longitudinal nerves, the uterus being wide and forked.
- *Anonchocephalus* Lühe, 1902, in which the strobila is segmented, head unarmed, testes situated mostly external to longitudinal nerves, and uterus very narrow.

The family is represented in India by a single species closely related to *Ancistrocephalus polyptera* (Leydig, 1853) Mont., 1890.

Genus ANCISTROCEPHALUS Lühe, 1899.

Synonym :—*Polyonchobothrium* Diesing, 1854.

The scolex is flattened and armed with small hooks. A pseudoscolex and neck always absent. External segmentation distinct, all the proglottides being broader than long. The genital ducts pass dorsal to the longitudinal nerves, the latter being situated a considerable distance from the margins of the segment. The testes are situated ventrally in two lateral fields, uniting posteriorly, and not extending laterally external to the longitudinal nerves. The genital pores are marginal, alternating ; vitellaria situated in the medulla in two lateral fields external to the longitudinal nerves, and connected by a layer of follicles immediately adjacent to the dorsal longitudinal muscle layer. A second layer of vitellaria, also

immediately adjacent to the longitudinal muscles, is sometimes present in the cortex dorsally. The ovary is bilobed. The uterus is a long, narrow, much coiled canal, its terminal portion

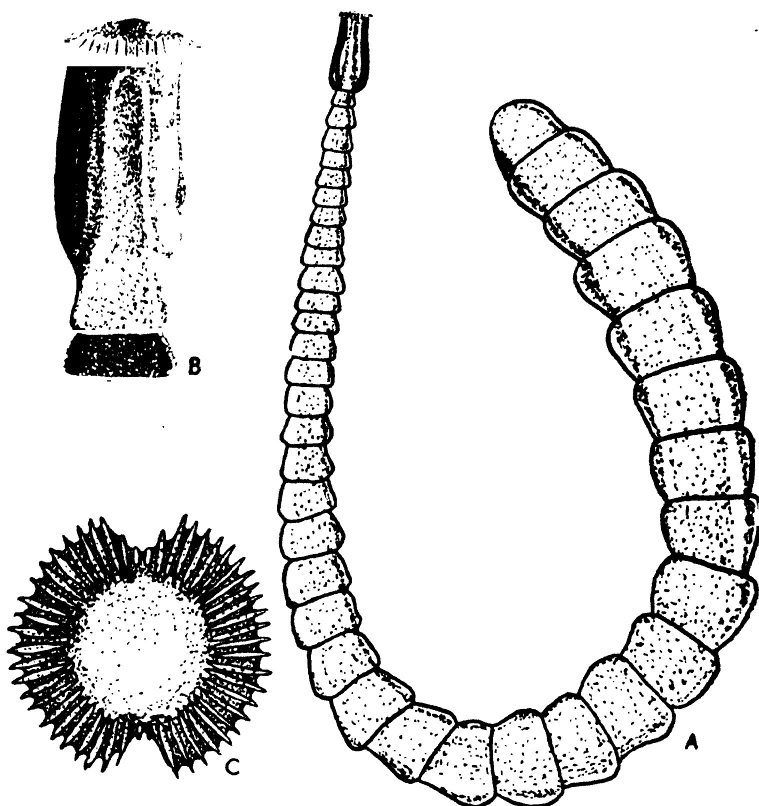


Fig. 12.—*Ancistrocephalus* sp. A, entire worm, ×about 18; B, head, ×75: C, head, viewed *en face*, ×140. (After Southwell.)

being dilated. The uterine pore is lateral and irregularly alternate. The eggs are thick-shelled. Adults in fish.

Type-species:—*Ancistrocephalus microcephalus* (Rudolphi, 1819).

Ancistrocephalus sp. (Fig. 12.)

Synonym:—*Ancistrocephalus polyptera* Southwell, 1913.

From *Ophiocephalus striatus* and *Labeo rohita*, Bengal, India. Southwell.

The worm measures 1·7 cm. in length and has a maximum breadth of 800 μ. Segmentation is definite and complete.

The scolex is somewhat rectangular in shape and bears two fleshy bothria; anteriorly it terminates in an umbrella-shaped rostral disc armed with about fifty-six straight, spindle-shaped spines, arranged in a single crown around its circumference, and having the appearance shown in fig. 12. A neck is absent. The first proglottis is almost square, and the latero-posterior margin of each proglottis overlaps the succeeding one. The internal anatomy of the worm is entirely unknown.

Southwell pointed out that this worm differed from *A. polyptera* in the number of spines and in the size of those spines situated immediately anterior to the bothria. Apparently only two species of the genus are known, namely, *A. microcephalus* (Rudolphi, 1819), from the sun-fish, *Orthagoriscus mola* (marine), and *A. polyptera* (Leydig, 1853), from *Polypterus bichir*, a fish the distribution of which is limited to the Nile and to the river basins of Tropical Africa which drain into the Atlantic. As pointed out by Southwell, the occurrence of this worm in a teleost is unique. The parasite cannot be referred to the genus *Bothriocephalus* because the bothria are well developed and segmentation is distinct. The worm properly belongs to the genus *Ancistrocephalus*, but the number and form of the hooks are not identical with those of the species *polyptera*. In the absence of any information relating to its internal anatomy, it has been thought inadvisable to make it the type of a new species.

Family III. PTYCHOBOTHRIIDÆ Lühe, 1902.

Scolex usually with two bothria, sometimes armed; a pseudoscolex may be present; segmentation complete, but sometimes obscured. Genital pores rarely marginal, almost always surficial, dorsal. Uterine pore ventral and situated in front of the genital pores. Receptaculum seminis, when present, a blind sac situated at the inner end of the vagina. Uterus never a rosette, generally a large sac with a small uterine duct. Eggs thin-shelled, usually not operculated.

Adults in fishes and mammals.

Type-genus :—*Ptychobothrium* Lönnberg, 1889.

Lühe (1902) erected this family, and cited *Bothriocephalus* Rudolphi, 1808, as the type-genus. His reasons for doing so are given in his paper.

This is directly contrary to the rules of nomenclature, and cannot possibly be accepted. The error has been copied by both Cooper (1918) and Meggitt (1924). If the family name, Ptychobothriidæ, is retained, then the type-genus must be *Ptychobothrium*. If, however, the type-genus of the family is

Bothriocephalus, then the family name must be Bothriocephalidæ. As it seems preferable to retain the family name, Ptychobothriidæ, I designate as the type-genus *Ptychobothrium* Lönnberg, 1889.

The family contains four genera. In two of these (*Bothriocephalus* Rud., 1808, and *Clestobothrium* Lühe, 1899) the uterus is sac-like, the bothria feeble and the receptaculum seminis absent in the former, whilst in the latter the head is spherical, the bothria are sunk in the scolex, and the receptaculum seminis is small. In the other two genera (*Ptychobothrium* Lönn., 1899, and *Taphrobothrium* Lühe, 1899) the uterus is a coiled canal; in the former the bothria are well developed, the vitellaria being situated in the cortical parenchyma, whilst in the latter the bothria are feeble and the vitellaria are in the medullary parenchyma.

Two doubtful species from India, which were placed in the genus *Bothriocephalus* Rud., 1808, are dealt with on page 58.

Genus BOTHRIOCEPHALUS Rudolphi, 1808.

Synonym:—*Dibothrium* Diesing, 1850.

Scolex elongated, with two bothria feebly developed. External segmentation indistinct, but marked by a tooth-like notching of the lateral border. Uterine pore median and ventral; male and female pores median and dorsal. Testes and vitelline glands continuous throughout the strobila. Vitellaria in the cortex. Receptaculum seminis absent. First part of the uterus a sinuous duct (uterine duct) opening into a large spherical sac (uterine sac or uterus s. str.).

Type-species:—*Bothriocephalus scorpii* (Müller, 1776).

(1) Bothriocephalus pycnomerus Woodland, 1924. (Fig. 13.)

From *Ophiocephalus marulius*, Allahabad, United Provinces, India. Woodland.

The worm measures up to 7·6 cm. in length and from 2 to 3 mm. in breadth. The scolex is about 1·1 mm. in length and 700 μ in maximum breadth. The anterior third of the scolex is narrower than the dilated posterior region, and terminates anteriorly in a truncated disc, the edges of which are drawn out into four lappets, each lappet being armed with about seventeen radially disposed, stout, rod-shaped spicules. In the middle region of the edge of each lappet the spicules attain a maximum length of 73 μ, but in the grooves between each pair of lappets they measure only 29 μ. The dilated posterior part of the scolex bears two shallow bothria. There is no neck. The lines of demarcation

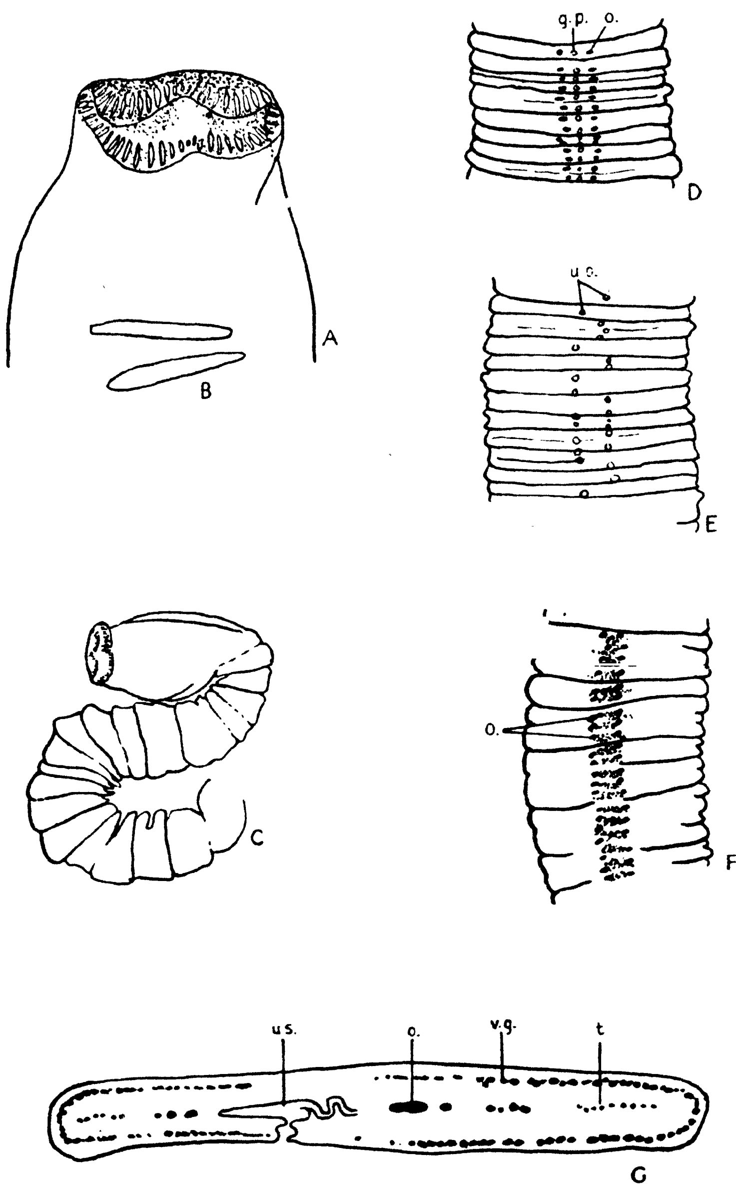


Fig. 13.—*Bothriocephalus pycnomerus.* A, head, × 56; B, scolex spicules, × 260; C, anterior end, × 17·5; D, dorsal aspect of worm, × 12; E, ventral aspect of worm, × 12; F, portion of immature worm, showing lack of correspondence between external segmentation and number of sets of genitalia, × 12; G, transverse section, in outline, of mature segment, × 28. (After Woodland, in 'Parasitology.')

of the proglottides one from another vary greatly in distinctness and correspondence with the sets of genitalia in different regions of the strobila. In the part where the genital rudiments first become distinct, each apparent proglottis contains from two to four sets of genitalia. In the area where the genitalia are mature there is also often no exact correspondence between the outlines of the segments and the sets of genitalia. In gravid segments it is also impossible to make the indistinct segments correspond with the uterine sacs. In certain places, however, the segments are distinct and appear to contain a single set of genitalia. The excretory system consists of two excretory canals situated one on each side of the strobila. The testes number from thirty to forty in distinct segments. The cirrus sac is large and muscular, and contains several coils of the ductus ejaculatorius. There is considerable variation with regard to the relative antero-posterior positions of the openings of the cirrus and uterine sacs. The ovary is a narrow bilobed organ situated at the posterior extremity of the proglottis. From it a short oviduct arises which opens into the oötype, which latter receives the openings of the vagina, the shell gland, and the vitellaria. From the oötype the tubular convoluted uterus arises and opens into a spacious, transversely elongated uterine sac. Neither the uterine sac nor its opening is ever situated in the median line: they are found irregularly either to the right or to the left. The uterine eggs measure about 44 by 26 μ. They are oval in shape, thin-shelled, and non-operculated.

This species resembles *B. histiophorus* Shipley, 1901, except that in the latter worm the scolex is apparently unarmed.

(2) **Bothriocephalus histiophorus** Shipley, 1901. (Fig. 14.)

Synonym:—*Bothriocephalus plicatus* Shipley, 1900.

From *Histiophorus* sp., Indian Ocean. Shipley. The length of the worm is not known; the longest fragment measured 20 cm., and it had a maximum breadth of 3 to 4 mm.

The scolex is unarmed; there are two longitudinal slit-like bothria, situated one dorsally and one ventrally, and a flat four-lobed "cap" measuring 1·5 mm., constricted near the posterior end. There is no neck. The proglottides are funnel-shaped, and have markedly salient angles, especially anteriorly. The ripe proglottis measures 160 μ in length and 500 μ in breadth. The cirrus opens medially and dorsally; close behind it the vagina opens, the pore being surrounded by a well-marked sphincter muscle; the uterine sac is pushed irregularly to the right or to the left, and its pore is distinctly not median. The vitellaria are situated in the cortical parenchyma close to the cuticle. The testes number fifty to seventy-five, and are

situated in the medulla. The ovary is a bilobed organ, and the oötype is conspicuous. A receptaculum seminis is absent. The uterine eggs measure 45 by 35 μ.

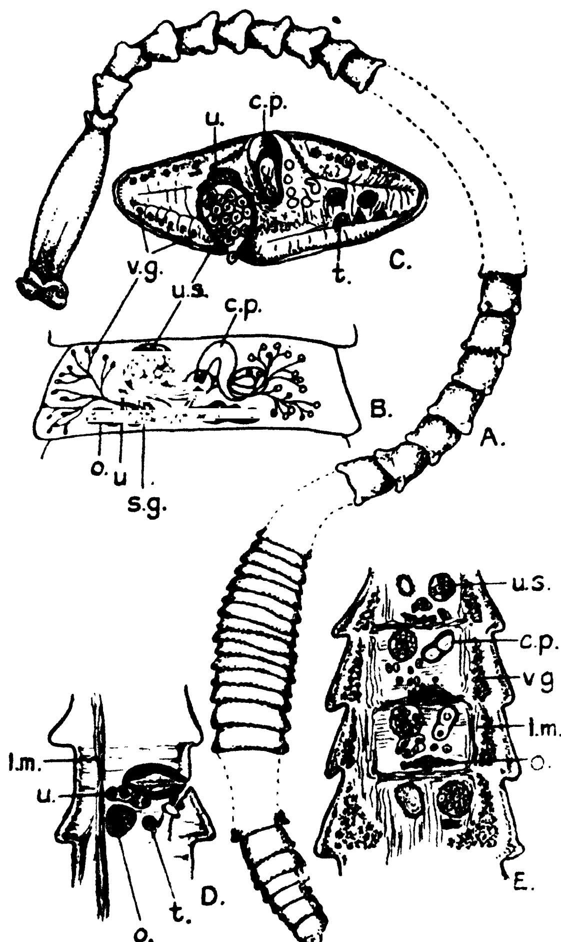


Fig. 14.—*Bothriocephalus histiophorus.* A, entire worm; B, segment; C, transverse section of segment; D, sagittal section of segment E, horizontal section of segment. Magnifications unknown. (After Shipley.)

No species of the families Amphicotylidæ Nybelin, 1920, and Echinophallidæ Schumacher, 1914, have been recorded from India.

Superfamily II. TETRARHYNCHOIDEA, nov.

Synonym :—Order *Trypanorhyncha* Diesing, 1863.

A full account of the history of the trypanorhynchids was published by the writer in 1929. As far as can be ascertained, Redi was the first to describe a worm belonging to this order. In 1684 he obtained larval tetrarhynchids from the liver, intestine, and testes of *Argentina sphyræna*. Gmelin (1790) gave the name *Echinorhynchus argentinæ* to the worms described by Redi. Rudolphi (1819) relates that :—"Redi described 8 worms with the head and half the body white. the rest of the body being yellow ; and again he described more than 50 worms white throughout. The size varies, extending in length beyond the breadth of four fingers across. When contracted they are smaller. They moved like snails, and they also carried four little horns on their head, or rather

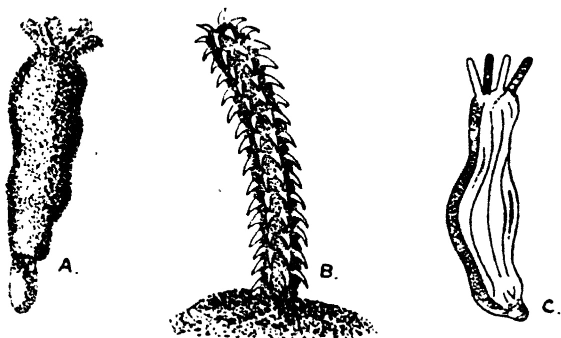


Fig. 15. *Echinorhynchus quadrirostris*. A, entire worm ; B, a proboscis. (After Goeze.)
Tentacularia coryphænæ. C, entire worm. Magnification unknown. (After Bosc.)

hard (?) and strong hooks, by the help of which they clung to the parts so strongly that he could not tear several away before he had cut away that part they were clasping. All seem to have been free or not enclosed in a sac, for of this sac no mention is made. Yet he states that certain worms lay hidden beneath the outer tunic of the intestine, liver, or ventriculus. . . . Some stuck at one time to the first stomach and at another to the tunic of the intestine and liver. That the species discovered by Redi (excellent man) is distinct, their different habitats, no less than their size, much greater than the rest, render probable." The identity of this parasite is quite uncertain.

Goeze (1782) gave the following description of another parasite which he named *Echinorhynchus quadrirostris* (fig. 15) :—

"Candidus, cylindricus, cauda rotunda, corpori intubulata, proboscide quadruplici retractili perechinata." His figures (3–5 on pl. xiii) show quite clearly that this worm was a larval tetrarhynchid. The host is *Salmo salar*. Zeder (1800) refers to this worm as *Echinorhynchus conicus*.

Bosc (1797) defined and gave a figure (fig. 15) of a parasite which he placed in a new genus named by him *Tentacularia*. His account reads:—"Body enclosed in a sac: apparently no mouth: four retractile tentacles on the head. The species . . . . found on the liver of *Coryphæna hippurus* had a longitudinally striated body. The sac containing it was two lines in length. *Echinorhynchus quadricornis* of Goeze (Linn. Syst. Nat. ed. Gmel. p. 3049, No. 35) should be included in this genus, which, at any rate, appears to be closely related to *Echinorhynchus*."

Apparently Bosc was in error here: he must have meant *E. quadrirostris* Goeze, 1782. There can be no doubt, however, that Bosc was right in including Goeze's species (i.e., *E. quadrirostris*) in his new genus *Tentacularia*. Bosc's parasite was a larval form, and no type-species was designated. In 1802 Bosc added a few details relating to his genus *Tentacularia*, and gave the species the name *Tentacularia coryphænæ*. He pointed out clearly that the genus *Tentacularia* differed from *Echinorhynchus* in having "its suckers in the form of retractile tentacles."

In 1809 Rudolphi established the genus *Tetrarhynchus*. He included it in his second order Acanthocephala, which comprised two genera only, viz., *Echinorhynchus* and *Tetrarhynchus*. It will be clear from the above that the name *Tentacularia* Bosc, 1797, has priority over *Tetrarhynchus* Rudolphi, 1809. Rudolphi in that year defined the genus *Tetrarhynchus* as follows:—"Body rounded, varied in form, proboscides evertible; hooks in series." He dealt with four species only, in the following order, and they were all larvæ, viz.:—

(1) *Tetrarhynchus appendiculatus*=*Echinorhynchus quadrirostris* Goeze, 1782.

(2) *Tetrarhynchus papillosus*=*Tentacularia coryphænæ* Bosc, 1797.

(3) *Tetrarhynchus elongatus*: this is the name he gave to the larva found by Redi in *Argentina sphyrænæ*, which Gmelin had previously named *Echinorhynchus argentinæ*.

(4) *Tetrarhynchus morrhua*: a name given by Rudolphi to larval forms from *Gadus morrhua* which Viborg and Abildgaard had previously named *Echinorhynchus quadrirostris*.

Rudolphi's description and figures give no clue as to what the adult worms are which are represented by the above larval forms. In 1810 he included in his genus *Bothriocephalus*

(division *armati*, Echinobothria) two species, viz., *Bothriocephalus corollatus* and *B. paleaceus*. The former was apparently a tetraphyllidean and the latter a tetrarhynchid. It appears certain, therefore, that Rudolphi's genus *Tetrarhynchus* contained at that time only larval forms.

Cuvier (1817) established the genus *Floriceps*, with the following characters:—"With four small proboscides or tentacles armed with hooks, by means of which they attach themselves to the viscera of their hosts. There is one which is quite common in rays, viz., *Bothriocephalus corollatus* Rudolphi, 7 inches in length. Its head is just like a flower." He defined the genus *Tetrarhynchus* as follows:—"They appear to be only *Floriceps* consisting simply of the head and two segments, instead of an elongated body and several segments. Very often one is found in the flesh of the tongue of the turbot and several other fishes (*T. lingualis* Cuvier)."

Rudolphi (1819) mentions a new genus which he called *Rhynchobothrius*, but he did not define it.

Van Beneden (1850) placed the genus *Tetrarhynchus* in his family Phyllorhynchiens, the latter being one of the three families into which he divided the order Tétraphylles.

Diesing (1850 and 1863) erected several new genera of tetrarhynchids, all of which have fallen into synonymy.

Carus (1863) accepted van Beneden's classification.

Cobbold (1864) defined the characters of his new family Tetrarhynchidæ as follows:—"Tetrarhynchidæ. The members of this family are easily recognized by the possession of four armed retractile proboscides attached to the head. The armature consists of several successive rows of sharply pointed recurved hooks, frequently amounting to several thousands. The head itself is usually more or less bilobed, each half supporting either one bipartite bothrium or else two separate fossæ. These cavities are also frequently supported on four petaloid appendages, which vary much in shape in the different species, and also in the same individual, according to the degree of contraction of the part. The head and neck are continuous, and usually about the same breadth as the body, the latter being sometimes even narrower than either the head or neck. The body is depressed, filiform, distinctly segmented, and usually of great length in the mature state, the reproductive orifices being situated at the lateral margin of the joints in an irregularly alternate manner."

Linton (1889) subdivided the family as shown below:—

Family Tetrarhynchidæ Cobbold, 1864
(=Subtribe Trypanorhyncha Diesing, 1863,
Subfamily Phyllorhynchinæ van Ben.).

Subfamily I. Dibothriorhynchinæ Mont., 1892
(= Dibothriorhynchidæ Diesing).

Genus 1. *Rhynchobothrium* Rudolphi, 1819 (= *Tetrarhynchus* of authors).

Genus 2. *Otobothrium* Linton, 1889

Subfamily II. Tetrabothriorhynchinæ Mont., 1888 (= Tetrabothriorhynchidæ Diesing, 1863).

Genus 1. *Tetrarhynchus* Rudolphi, 1809.

Genus 2. *Syndesmobothrium* Diesing, 1854.

Lönnberg in 1889 erected the Cœnomorphinæ as a subfamily of the Tetrarhynchidæ. Type and only species, *Cœnomorphus grossus* (Rud.)=*Tetrarhynchus linguatulus* (van Ben.)=*T. solidus* Drummond, 1838. The principal characters of the subfamily are: (1) the presence of a double set of genitalia in each segment, and (2) the fact that the worms are very stout and muscular.

Vaullegeard in 1899 published a very able revision of the tetrarhynchids, and his work deserves to be much more widely known than it is at present. He concludes that they form such a homogeneous group that their division into genera is well-nigh impossible; but he divides them into two sections, viz.:—

(1) TETRARHYNCHUS LINGUALIS Section.

This included all those species in which the larva develops within a vesicle. It contains *Tetrarhynchus quadrirostris* (Goeze, 1782); *T. lingualis* Cuvier, 1817; *T. infulatus* (Molin, 1858); *T. bisulcatus* (Linton, 1889); *T. robustus* Linton, 1890, and *T. lintoni*, Vaullegeard, 1899 (=*T. tenuis* Linton, 1890). It is curious to note that all species in this section have two characters in common, viz., (*a*) the posterior part of the head is produced into a collar-like structure which overhangs the anterior segments. and (*b*) the hooks on the proboscides are numerous, minute, practically all alike, and equal in size.

(2) TETRARHYNCHUS ERINACEUS Section.

This included all those species in which the larvæ develop within a bladder. It contains the great majority of tetrarhynchids.

Between the above two sections he placed an intermediate series which he termed the "*viridis*" section. It included *Tetrarhynchus megacephalus* Rudolphi, 1819; *T. tetrabothrius* (van Beneden, 1849); *T. caryophyllus* (Diesing, 1850); *T. viridis* Wagener, 1854, and *T. crenacollis* (Linton, 1890).

Braun (1900) included the following genera in the order Trypanorhyncha, viz.: *Rhynchobothrius* Rudolphi, 1819; *Dibothriorhynchus* Blainville, 1828 (=*Cœnomorphus* Lönnberg, 1889); *Tetrarhynchobothrium* Diesing, 1850;

Synbothrium Diesing, 1850; *Aspidorhynchus* Molin, 1858; *Abothros* Welch, 1876; and *Otobothrium* Linton, 1890.

Lühe (1910) defined the order Trypanorhyncha thus:—"Cestodes whose scolex is usually continued into a head-stalk; with two or four bothridia at whose apical end are four armed extensile proboscides. When retracted (with the assistance of a retractor which runs in their interior and is inserted into their anterior end) each is drawn back into a proboscis sac; this corresponds in thickness and length with the proboscis itself, and represents a direct continuation of the proboscis into the anterior end of the scolex and head-stalk. At its inner end the sheath passes directly into the visibly thicker, sharply delineated, egg-shaped or sausage-shaped sac, whose contraction brings about the extrusion of the proboscides. External segmentation complete. Formation of segments as in Tetraphyllidea. Mature in stomach or spiral valve of selachians; larvæ found in all kinds of marine animals. In fresh water only a few species are found in the larval condition as parasites of teleosts. No details of the development of the larvæ are known." He distinguished two families, viz.:—

1. Larva encysted; proboscis long, slender, cylindrical; whole body not massive or muscular ..	Tetrarhynchidæ.
2. Free larvæ, not encysted; proboscis short, almost semi-globular or club-shaped; whole body robust or muscular	Cœnomorphidæ.

He ascribed the following characters to the family Tetrarhynchidæ Cobbold, 1864:—"Scolex with long, slender, cylindrical, very mobile proboscides, with two or four very mobile bothridia more or less leaf-like. Head-stalk present. Strobila slender, with little muscular development, often transparent. Segments, when mature, longer than broad, easily detachable; in each segment a single set of genital organs. Uterus apparently without primary pore. Ripe eggs, as in Tetraphyllidea, escape through dehiscence. In spiral valve of selachians; larvæ in turtles, bony fish, cephalopods and decapods." He added that nothing was known regarding the systematic division of the family.

He defined the family Cœnomorphidæ Lühe (1910) as follows:—"Scolex very robust, with short, thick proboscides, semi-globular or club-shaped, with two simple bothridia sunk into the scolex like a pit or a split, and with edges which hardly protrude; no head-stalk. Strobilæ robust and very muscular, up to 4 mm. in thickness and not transparent; segments when mature much broader than long and not separating off. In each segment there are two sets of genital organs; uterus with a special pore opening ventrally and having its own muscular system. Mature in stomach of sharks; larvæ, not

encysted, found in bony fish. There is only one genus with one species, viz., *Cœnomorphus grossus* (Rud.)=*Tetrarhynchus solidus* =*T. linguatulus*."

Pintner (1913), in dealing with the tetrarhynchids in general, pointed out that so little was known regarding the anatomy of the various species that it was impossible to deal extensively with the family. He recognized three groups, viz. :—

1. With a true uterine pore present .... *T. viridis* group.
2. With an involuted apparent pore, not found in the anterior segments .... *T. ruficollis* group.
3. Segments dehiscent, no uterine pore either primary or secondary .... *T. tenuis* group.

In addition, he defined, in very elaborate detail, the characters of six genera, four of which were new. The same author adopted the following terminology :—The head is *craspedote* where there is a division between it and the neck ; it is *acraspedote* where the division is absent. Ripe segments are *anapolytic* when they remain attached to the strobila, but *apolytic* when they automatically separate from it. Gravid segments are *euapolytic* when they separate from the chain and continue to grow, but *hyperapolytic* if they separate from the strobila before they are mature, and especially if they do so before the uterus is developed.

Poche (1926) classified the Trypanorhyncha as follows :—

Class Cestoidea.

Subsubclass I. Amphilinoinei Poche, 1926.

Subsubclass II. Tænioinei Poche, 1926.

Order I. Bothriocephalidea Poche, 1926.

Order II. Echinobothriidea Poche, 1926.

Order III. Tetrarhynchidea Poche, 1926.

The latter he subdivided as follows :—

Suborder I. Haplobothriinea Poche, 1926.

Family Haplobothriidæ Meggitt, 1924, containing only *Haplobothrium globuliforme* Cooper, 1914.

Suborder II. Tetrarhynchinea Poche, 1926.

Subtribe 1. Aporhynchoinæ Poche, 1926.

Family Aporhynchidæ Poche, 1926, containing only *Aporhynchus norvegicus* (Nybelin, 1918).

Subtribe 2. Tetrarhynchoinæ Poche, 1926.

Family Tentaculariidæ Poche, 1926, with the following genera :—

(1) *Tentacularia* Bosc (= *Tetrarhynchus* Rud.) ; (2) *Eutetrarhynchus* Pintner ; (3) *Tetrarhynchobothrium* Diesing ; (4) *Stenobothrium* Diesing ; (5) *Lakistorhynchus* Pintner ;

(6) *Acoleorhynchus* Poche, 1926 ; (7) *Nybelinia* Poche, 1926 (for *Aspidorhynchus* Molin) ; (8) *Synbothrium* Diesing ; (9) *Abothros* Welch ; (10) *Floriceps* Cuvier ; (11) *Wagneria* Monticelli ; (12) *Halysiorhynchus* Pintner ; (13) *Sphyriocephalus* Pintner ; (14) *Dibothriorhynchus* Blainville ; (15) *Otobothrium* Linton.

Guiart (1926) placed all the tetrarhynchids in the order Rhynchobothriens Dujardin, 1845; this he divided as follows:—

Suborder I. Acystidea Guiart, 1926.

Contains all tetrarhynchids the larvæ of which belong to *Tentacularia*. Head free, not in a vesicle, bothridia dorso-ventral ; proboscides usually rather short, emerging from top of head between bothridia, and armed with small similar hooks. Bulbs short and usually immediately behind bothridia. Neck sometimes has an annular fold or collar.

Family I. Bouchardidæ Guiart, 1926.

Genus *Bouchardia* Guiart, 1926.

Type-species :—*Bouchardia crassiceps* (Diesing, 1850).

Family II. Rufferidæ Guiart, 1926.

Genus 1. *Rufferia* Guiart, 1926.

Type-species :—*Rufferia tubiceps* (Leuckart, 1819).

Genus 2. *Pierretia* Guiart, 1926.

Type-species :—*Pierretia carchariæ* (Linstow, 1878).

Suborder II. Cystidea Guiart, 1926.

Contains all tetrarhynchids the larvæ of which belong to *Anthocephalus*.

Head enclosed in a vesicle, which may bear a very long caudal appendage. Bothridia dorso-ventral or lateral ; proboscides long, armed with hooks often dissimilar ; bulbs generally long and situated behind head.

Family III. Vaullegeardidæ Guiart, 1926.

Genus I. *Vaullegeardia* Guiart, 1926.

Type-species :—*Vaullegeardia moniezi* (Railliet, 1899).

Family IV. Lacistorhynchidæ Guiart, 1926.

The author did not mention any genera belonging to this family.

Woodland (1927) united the orders Tetraphyllidea and Trypanorhyncha, together with the family Proteocephalidæ, into one order, viz., Tetraphyllidea (sens. nov.). He stated

that the Trypanorhyncha (which he referred to as the family Tetrarhynchidæ Cobbold) have the following characteristics :—Head with four proboscides, a distinct internal layer of longitudinal muscle bundles, concentrically arranged vitellaria, and a vagina situated ventrally to the uterus and cirrus sac.

The vitellaria are usually arranged concentrically, but in a few cases they definitely consist of two marginal strands only. The longitudinal muscle fibres are not always either distinct or internal. In some species the fibres are scattered through the cortical parenchyma, whilst in others they are collected into large bundles which occupy the major portion of the cortex. It remains to be seen whether the vagina is constantly situated ventrally to the uterus and cirrus pouch or not. He also suggests the inclusion of *Adelobothrium ætiobatidis* Shipley, 1900 (=*Tylocephalum marsupium* Linton, 1916), in the family Tetrarhynchidæ because the vitelline glands are concentric, even though the head does not bear proboscides.

Pintner (1928) placed all the tetrarhynchids in one family Tetrarhynchidæ in his Order II. Cestodes (s. str.).

Essex (1928) records from the livers of five specimens of *Amieurus nebulosus* taken from the Mississippi, Minnesota, eight cysts measuring about 700 by 660 μ, each containing a larval cestode possessing four protrusile proboscides without hooks or spines, and, so far as could be ascertained, without accessory bothria or acetabula. The character of the scolex suggests that the larvæ probably belong to the order Trypanorhyncha. Apparently, however, they differ from all other species of this order in that the proboscides are unarmed ; whether this feature persists in the adult worm remains to be seen, and the larva cannot be definitely classified in the present state of our knowledge of this form.

Proposed Classification.

Superfamily II. Tetrarhynchoidea, nov.

Family I. Tetrarhynchidæ Cobbold, 1864.

Synonym :—Tentaculariidæ Poche, 1926.

Genera :—*Tetrarhynchus* Rudolphi, 1809.
Tentacularia Bosc, 1797.
Gymnorhynchus Rudolphi, 1819.
Otobothrium, Linton, 1890.

Family II. Cœnomorphidæ Lühe, 1910, emended.
Genus *Cœnomorphus* Lönnberg, 1889, emended.

Family III. Haplobothriidæ Meggitt, 1924.
Genus *Haplobothrium* Cooper, 1914.

Of uncertain systematic position :—

Aporhynchus Nybelin, 1918.

The above six genera are recognizable by the following general characters :—

1. *Tetrarhynchus* : with four bothridia lying parallel to strobila, except in one species, viz., *T. herdmani*.
2. *Tentacularia* : with two lateral bothridia which may be entire or divided to a varying degree.
3. *Gymnorhynchus* : with four terminal bothridia arranged in the form of a cross, without ciliated pits.
4. *Otobothrium* : in which there are either two bothridia, each bearing a pair of ciliated pits, or four bothridia each with a single ciliated pit.
5. *Cœnomorphus* : in which there is a double set of genitalia in each segment.
6. *Haplobothrium* : in which the genital pores are ventral.

The characters of the superfamily, families, and genera are given below :—

Superfamily II. Tetrarhynchoidea, nov.

Head with two or four bothridia and bearing four protrusile proboscides armed with hooks ; segmentation complete. Genital organs as in the Phyllobothrioidea (except in *Haplobothrium*). Vitelline glands usually encircling the segment, but may be paired and marginal ; they lie either externally or internally to the longitudinal muscles ; the latter are either collected in definite bundles or scattered as separated fibres in the cortex. Primary uterine pores either present or absent. Adults in elasmobranch fishes and occasionally in teleosts. Larvæ in teleosts, reptiles, and invertebrates. With three families.

Family I. Tetrarhynchidæ Cobbold, 1864.

With a single set of genitalia in each segment. Genital pores marginal. Worms more or less fragile. Parasitic in marine and fresh-water fishes.

Type-genus :—*Tetrarhynchus* Rudolphi, 1809.

Family II. Cœnomorphidæ Lühe, 1910, emended.

With a double set of genitalia in each segment. Genital pores marginal. Strobila stout and muscular. Parasitic in marine and fresh-water fishes No species of this family have been recorded from India.

Type-genus :—*Cœnomorphus* Lönnberg, 1889.

Family III. Haplobothriidæ Meggitt, 1924.

This family contains one genus only, with a single species, viz., *Haplobothrium globuliforme* Cooper, 1914. In this worm the scolex of the primary strobila is reduced and consists of a club-shaped organ bearing four protrusile armed proboscides as in other species of Tetrarhynchoidea. The spines continue over the anterior portion of the scolex. Segmentation commences a considerable distance behind the head and the segments are few and very much longer than broad. Later on each of these segments breaks away from the parent strobila and becomes secondarily segmented; the secondary anterior segment of each fragment bears a pseudoscolex in the form of two bothria, one dorsal and one ventral, as in many species of Dibothriocephaloidea. The borders of the terminal disc of the secondary scolex and of the posterior auricular appendages of both scolex and anterior segments are provided with minute spines which disappear with the appendages further back. This secondary segmentation is marked before each primary segment separates from the original strobila. A single set of genital organs in each segment; genital and uterine pores situated on the flat (ventral) side. Vitelline glands and testes in the medullary parenchyma, both internal to the nerve trunks. Testes in two lateral fields, with vitellaria arranged cylindrically around them, leaving clear areas opposite the central genital ducts. Uterus divided into a coiled proximal uterine duct and a large uterine sac.

This species possesses characters which ally it to both the Tetrarhynchoidea and the Dibothriocephaloidea. The four armed proboscides are typically tetrarhynchid, whilst the presence of ventral genital pores and pseudobothria at the exterior extremity of the secondary strobila indicate its relationship to the Dibothriocephaloidea *.

Found in the intestines of fish (*Amia calva*) in Canada and America. The worm has not been recorded from India.

Type-genus :—*Haplobothrium* Cooper, 1914.

Of uncertain systematic position :—

Genus *Aporhynchus* Nybelin, 1918.

This genus contains only a single species, viz., *Aporhynchus norvegicus* (Nybelin, 1918), the characters of which are : the entire absence of proboscides ; the unpaired vitelline duct forks ; the scolex is acraspedot, there are four bothridia ; the external seminal vesicle is very muscular, the cirrus very thick and muscular ; a pseudouterine opening present.

Having regard to the fact that, amongst other things, the position of the genital pores in *Haplobothrium* has been con-

* It is further related to the Dibothriocephaloidea in that its life-history is similar to that of *Dibothriocephalus latus*.

sidered sufficient to warrant the erection of a family, and even a suborder, to contain it, and, similarly, that the presence of double genital organs in *Cænomorphus* is also regarded as of family value, one feels justified in considering that the differential characters named above are, if not adequate, at least useful generic distinctions.

It has been previously noted that Redi described, but did not name, a number of larval tetrarhynchids, and that Goeze described others under the name *Echinorhynchus quadrirostris*; Bosc, however, was the first to separate his species from the genus *Echinorhynchus* and to apply the name *Tentacularia* to those forms with four proboscides. The name *Tentacularia* Bosc, 1797, therefore has priority, and Poche, in 1926, erected a family Tentaculariidæ, containing fifteen genera, which comprises almost all the known species. Worms of this family are, however, commonly called tetrarhynchids.

Cobbold (1864) erected the family Tetrarhynchidæ, and for this reason the superfamily is named Tetrarhynchoidea, although it is true that the name *Tentacularia* has precedence. It is impossible to decide from Bosc's crude figure of *Tentacularia coryphænæ*, obtained from a dolphin, whether the head of his species had two or four bothridia.

Linton, in the years noted below, recorded the following forms from the common dolphin (*Coryphæna hippurus*), viz., (1897) *Tetrarhynchus bicolor* Bartels, a species with four bothridia; (1901) *T. bicolor* Bartels, and *Rhynchobothrium* sp., a species with two bothridia; (1905) *T. bicolor* Bartels, and *Rhynchobothrium speciosum* Linton, 1897, a species with two bothridia. It will be noted that the larval forms recorded from the dolphin comprise species in which the head bears two bothridia and forms in which four bothridia are present, and of these it is impossible to decide which was the one obtained by Bosc. Of these larval forms, *R. speciosum* has been described and figured better than the rest, and I therefore designate *Rhynchobothrium speciosum* Linton, 1897, as being synonymous with *Tentacularia coryphænæ* Bosc, 1797, the type-species of the genus.

The two genera *Tentacularia* and *Tetrarhynchus* are separated in a most arbitrary manner by the fact that in the former there are two bothridia, simple or partly divided longitudinally, whilst in the latter there are four bothridia. This distinction has, however, a very limited morphological significance. The only justification for it is that it facilitates the identification of species. Like every other character, it fails in some instances, for, although it is easy to refer worms with two or four bothridia to their respective genera, there are a few species in which each bothridium is only partially divided, and it may then become difficult to decide whether there are two or four bothridia. Another similar complication may arise when a single

bothridium fuses with the head, leaving its two lateral margins free, as in *Otobothrium balli* Southwell, 1929, and *Tetrarhynchus matheri* Southwell, 1929. In such cases the four lateral margins of the two bothridia present the appearance of four bothridia. Such forms as these are to be regarded as intermediate, and are difficult to classify.

It has been found necessary to include in the genus *Tetrarhynchus* one species in which the head bears only two bothridia, namely, *Tetrarhynchus herdmani* Shipley & Hornell, 1906. The reason why this is so is owing to the fact that the eight known species which are referred to the "*lingualis*" group (see p. 74) are very closely related to each other, being characterized by (1) the posterior part of the head overhanging the neck in the form of a collar; and (2) the hooks on the proboscides being practically all alike and extremely minute except perhaps in the case of *Tetrarhynchus equidentatus*.

All the species possess four bothridia except *Tetrarhynchus herdmani*. It seemed quite undesirable to split up such a very definite natural group as this and to distribute the species into two genera, namely, those with four bothridia in the genus *Tetrarhynchus* and those with two bothridia in the genus *Tentacularia*. Therefore this species, although possessing only two bothridia, is retained in the genus *Tetrarhynchus*.

Family I. TETRARHYNCHIDÆ Cobbold, 1864.

Genus I. TETRARHYNCHUS Rudolphi, 1809.

Small to medium sized worms; head with four bothridia lying parallel with the body and having their sucking surfaces facing externally.

Type-species :—*Tetrarhynchus appendiculatus* Rud, 1809.
Synonyms :—*Echinorhynchus quadrirostris* Goeze, 1782.
Echinorhynchus conicus Zeder, 1800.

The adult worm *Tetrarhynchus appendiculatus* is not known. The host of the larva is *Salmo salar*.

The "*Tetrarhynchus lingualis*" group includes the following species in which (*a*) the head is produced backwards into a prominent collar * which overhangs the anterior part of the strobila, and (*b*) the hooks on the proboscides are almost always minute and of equal size, viz. :—

T. lingualis Cuvier, 1817.
T. bisulcatus (Linton, 1889), Linton, 1897.

* In one species of the genus *Otobothrium*, namely, *O. insigne*, the head also bears a collar, an indication that the hard-and-fast distinctions which are made between genera cannot be pushed too far.

T. robustus Linton, 1890. Synonym: *T. narinari* MacCallum, 1917.
T. tenuis Linton, 1890.
T. perideræus Shipley & Hornell, 1906.
T. equidentatus Shipley & Hornell, 1906.
T. herdmani Shipley & Hornell, 1906.
T. palliatus Linton, 1924.

As the principal differences between the nine species dealt with below have reference to the size and shape of the hooks on the proboscides, it is not possible to provide a key.

(*a*) Adult Forms.

(1) **Tetrarhynchus perideræus** Shipley & Hornell. (Fig. 16.)

From (1) *Carcharias gangeticus*, Pearl Banks. Shipley and Hornell. (2) *Ginglymostoma concolor*, Pearl Banks, Ceylon. Pearson.

Shipley and Hornell described this worm as follows:—"This species was present in large numbers in the small intestine of *Carcharias gangeticus*. The head and a peculiar extension of the head in this species is a well-marked shade of dark grey, which contrasts vividly with the matt-white of the rest of the body. Even in the stained and mounted specimens peculiar coloured granules can be recognized, which doubtless give rise to this colour in the living animals. This is a big species, some specimens attaining a length of 70 mm., possibly more, as the bottle in which they travelled was full of segments. The width varies, but is never great, and even the head never exceeds about 1·3 mm. The head bears two lappets, but they are so divided in the centre as to appear as four. They are very compressed into the head and do not stand out. They appear rather puckered at their edges. The proboscides are slender and bear oblique rows of very minute teeth, all of uniform size. The proboscis tubes and proboscis sheaths are alike short. The head is produced backwards into a very characteristic collar which overhangs and embraces the anterior part of the body. This is a very marked feature. There is a fairly long neck, the first trace of segmentation occurring some way behind the posterior limit of the collar. The proglottides have straight sides and, except at the posterior end, there is no sign of the cuticle being indented between them. One peculiarity is that the body, usually about the middle of its length, is thrown into coils and twists of a very characteristic form. In the anterior proglottides one sees a central stained part, possibly the uterus; posteriorly, however, the scattered testes are visible, and the vas deferens

and penis, represented sometimes by a clear area, runs from about the centre of the anterior border of each proglottis to the middle of either side, right or left, irregularly alternating."

In 1924 the writer gave a brief description of the anatomy.

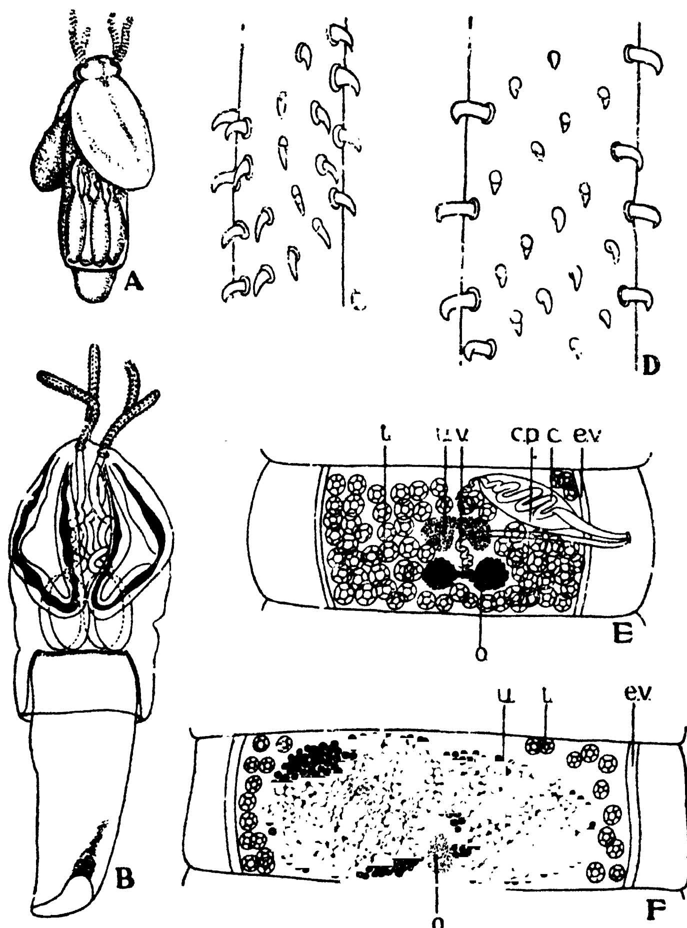


Fig. 16.—*Tetrarhynchus perideræus.* A, larva, magnification unknown; B, head, × 37; C, proboscis hooks, × 330; D, proboscis hooks, × 500; E, mature segment, × 46; F, gravid segment, × 46. (After Southwell.)

As more material has since been obtained, a fuller account is now given.

The worm measures up to 7 cm. in length and 1·7 mm. in breadth. It is composed of a large number of segments with

convex margins, all of which are much broader than long. The last gravid segment measured 500 μ in length and 1·7 mm. in breadth. The genital pores are irregularly alternate, and are situated subventrally a little in front of the middle of the lateral margin. In this respect it differs from *T. lingualis* Cuv., 1817, and *T. bisulcatus* Linton, 1889. There is no neck.

Head. The head measures about 1·3 to 1·75 mm. in length and from 800 μ to 1 mm. in breadth. The four bothridia measure from 900 μ to 1 mm. in length, and their posterior extremities lie over the centre of the proboscis sacs. The latter measure 350 μ in length by 180 μ in breadth. The proboscides are short; within the head they form about two coils, while their free portions are also short. They are armed with a number of small, simple, delicate hooks which have their tips slightly recurved, and which measure from 10 to 12 μ. These hooks are arranged spirally, there being 12 hooks in that portion of the spiral which completely encircles the proboscides once, so that 6 hooks are visible in each half-spiral. The posterior part of the head is produced into a remarkable fold or collar which encircles the anterior extremity of the strobila.

Testes. The testes vary in number from 60 to 70, they occupy the entire dorsal area within the excretory vessels, and a few testes are situated posteriorly to the ovary.

Vas deferens. The cirrus pouch is not conspicuous; it lies anteriorly to the vagina and median to the excretory vessels; it communicates with the exterior, and opens subventrally by means of a long narrow duct. In the median direction it extends almost half-way across the segment, its median extremity being closely apposed to the anterior extremity of the segment; no spines were observed on the cirrus. The vas deferens lies coiled within the cirrus pouch, near the median extremity of which it dilates into a seminal vesicle.

Ovary. This is peculiar in being situated a little distance from the posterior extremity of the segment, and in being small and dumb-bell-shaped; it stains very deeply and the two lobes are very compact. The vagina runs posteriorly to the cirrus pouch.

The *vitelline glands* are very scanty, and consist of single acini practically encircling the segment. The rudiment of the uterus is represented by an oval organ situated immediately in front of the ovary. Unlike what occurs in most other tetrarhynchids, the uterus forms early and consists of two lateral pouches in communication with each other, which continue to grow until they completely fill the segment.

The *eggs* are oval, and measure 34 by 23 μ; the shell does not bear filaments.

Cuvier erected *T. lingualis* in 1817; Shipley and Hornell have described three and Linton four other species of tetrarhynchids in which the posterior part of the head is produced into a peculiar fold or collar which overhangs and covers the anterior part of the neck, as in *T. lingualis*, and in all the eight species the hooks are minute and practically equal. The principal points relating to the three Indian species are tabulated below.

Larval forms of this species have been obtained from *Balistes mitis* and *B. stellatus*.

The cysts are semi-transparent, oval, with broad extremities, and flattened, measuring about 6 by 4 mm. The larval head measured 1·3 mm. in length.

(2) **Tetrarhynchus equidentatus** Shipley & Hornell, 1906. (Fig. 17.)

From *Dasybatus walga*, Pearl Banks, Ceylon. Shipley and Hornell.

"This is, I think, the largest *Tetrarhynchus* I have seen, and it is certainly very large to come from the alimentary canal of an elasmobranch. Unfortunately but one specimen was taken, and this measured 4·7 cm. in length, not a very great length; but it is the breadth which gives the magnitude to

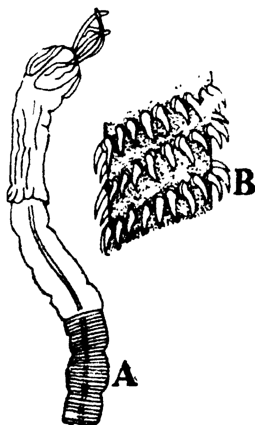


Fig. 17.—*Tetrarhynchus equidentatus.* A, head, ×4; B, proboscis hooks, ×50. (After Shipley and Hornell.)

this animal. It is almost uniformly 3 mm. broad from one end to the other, though it increases very slightly as we pass backwards, but the last proglottis is narrowed. It is perhaps 0·3 mm. thick.

"Compared with the size of the body, the head is very small, and the muscular sheaths come right up to the anterior end of it, and thus there are no more or less coiled tubes between them and the base of the exerted proboscides. The proboscides bear spiral or rather obliquely placed rings of hooks; the hooks are all of precisely equal size and most regularly arranged. They are 0·049 mm. in length. The head bears laterally well-marked lappets or bothridia. It is succeeded by an unsegmented region which is about 2 to 2·5 times the size of the head. This region terminates, as in *Tetrarhynchus herdmani*, in a well-marked collar with somewhat scalloped edge. The collar hangs back and overlaps the body region.

"The divisions between the proglottides are anteriorly very insignificant, but they soon become distinct, and the proglottides become a little longer. The total number is between one and two hundred; but they are never very long, never even square. The posterior proglottides are always some six or seven times as long as they are broad, and the anterior perhaps twice as much again. Their edges are rounded; there is no trace of overlapping, and in the latter half of the body the reproductive organs cause an opaque patch in each segment." (*Shipley & Hornell.*)

Poche (1926), as a result of Shipley and Hornell's statement that the proboscis sacs extend to the anterior extremity of the head, has separated this species from the group and made it the type of a new genus which he names *Acoleorhynchus*. Pintner (1928) figures the proboscis sacs situated almost posteriorly, and rightly retains the species in the genus *Tetrarhynchus*.

Shipley and Hornell figure the species as possessing two bothridia.

(3) **Tetrarhynchus herdmani** Shipley & Hornell, 1906. (Fig. 18.)

From *Dasybatus walga* and *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Shipley and Hornell.

"The second species to [sic] *Tetrarhynchus*, found in the alimentary canal of *Trygon walga*, and later in the same position in *Rhynchobatus djeddensis*, is a long and comparatively slender one. We had only three or four specimens, which averaged only about 30 mm. in length. The head is small, only about 1 mm. in length. It has two well-developed lappets which, as usual, are very contractable and extensile. The four proboscides emerge from very short muscular sheaths, which lie near the posterior limit of the head. Instead of being half as long as the head, as is often the case in the Tetrarhynchidæ, they are perhaps from one-twelfth to one-tenth

the head length. The proboscides which emerge from them are slender and covered with minute teeth, all of the same size, arranged in spiral rows. The teeth are about 0·01 mm. in length.

"The most characteristic feature of this cestode, but one which it shares with *T. equidentatus* . . . is a peculiar fold or collar which hangs back from the head and covers the anterior part of the neck. This collar seems to be very extensile. In the figure drawn from the live specimen, its border of free edge is scalloped, but in the specimens in spirit the collar seems more retracted and the free edge is smooth and undivided.

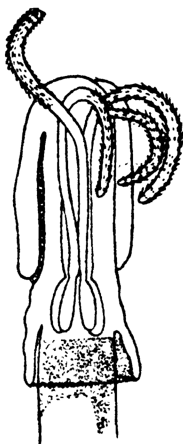


Fig. 18.—*Tetrarhynchus herdmani.* Head. × 60.
(After Shipley and Hornell.)

"The neck is very short. Almost immediately after the head the proglottides are indicated by sharp lines. There are some 80 to 100 proglottides present, all separated from one another by clear, horizontal, and in no case concave lines. Till the proglottides become packed with eggs, the lateral contours are also straight and parallel; there is no overlapping. Thus the cestode does not increase in width until we get to the posterior proglottides, and in these the presence of eggs entails a slight lateral swelling, so that this end is almost moniliform. The eggs are about 0·07 mm. in length.

"In the centre of each of the last half-dozen proglottides is a large clear place. This may possibly be the remains of the genital atrium, and, if so, this is median.

" *Tetrarhynchus herdmani* is characterized by having a small head, well-developed bothridia, short muscular proboscis sheaths, one-tenth to one-twelfth the length of the head, teeth on proboscis, uniform in spiral lines, 0·01 mm. in length, well-developed collar, 60 to 100 proglottides, most with parallel sides." (*Shipley & Hornell.*)

Table showing the Principal Characters of the Three Indian Species of the " lingualis " *Group.*

	T. perideræus.	*T. herdmani.*	*T. equidentatus.*
Length of worm ..	7 cm.	3 cm.	4·7 cm. × 3 mm.
No. of segments ..	Very numerous.	80–100.	100–200.
Position of genital pore.	A little in front of middle.	Middle.	?
Hooks	10 μ.	About 10 μ.	49 μ.
Proboscis sacs... ..	Half length of head ; short oval in centre of head.	Short, $\frac{1}{10}$–$\frac{1}{12}$ length of head. Posterior.	Long, extending anterior to extremity of head.
Bothridia ..	4	2	4

(4) **Tetrarhynchus shipleyi** Southwell, 1929. (Fig. 19.)

From *Ginglymostoma concolor*, Pearl Banks, Ceylon. Southwell.

The worms are very delicate and thread-like ; the largest measure 2 cm. in length, 800 μ in breadth, and contain 34 segments ; most of the specimens, however, measure about 1 cm. in length by 300 μ in breadth. None of the specimens are fully gravid. In the most mature worms the testes are developed and the rudiments of the ovary can be seen. The last segment measures about 1·45 mm. in length and 350 μ in breadth. The genital pore is situated laterally in the posterior fourth of the segment. There is a comparatively long neck.

Head. The head varies in length from 2 to 3·5 mm. In the latter the breadth across the proboscis sacs was 480 μ, and the breadth anterior to the sacs was 320 μ. The breadth across the bothridia varies according to whether the bothridia are viewed dorso-ventrally or laterally ; in the largest specimens the breadth was 720 μ. There are four bothridia having a length of about 750 μ. They have slightly thickened margins which bear numerous minute cilia ; in low-power magnification they can be seen as a dark line running parallel to the margin of the bothridia. Evidently they are deciduous, for in

one head both the hooks on the proboscides and the cilia were missing.

The proboscis sacs are short and stout, measuring about 540 μ in length and 145 μ in breadth. The proboscides are very long and coiled within the head, and their free portion is also very long. The hooks are all delicate and of various shapes and sizes, as shown in fig. 19, the largest measuring

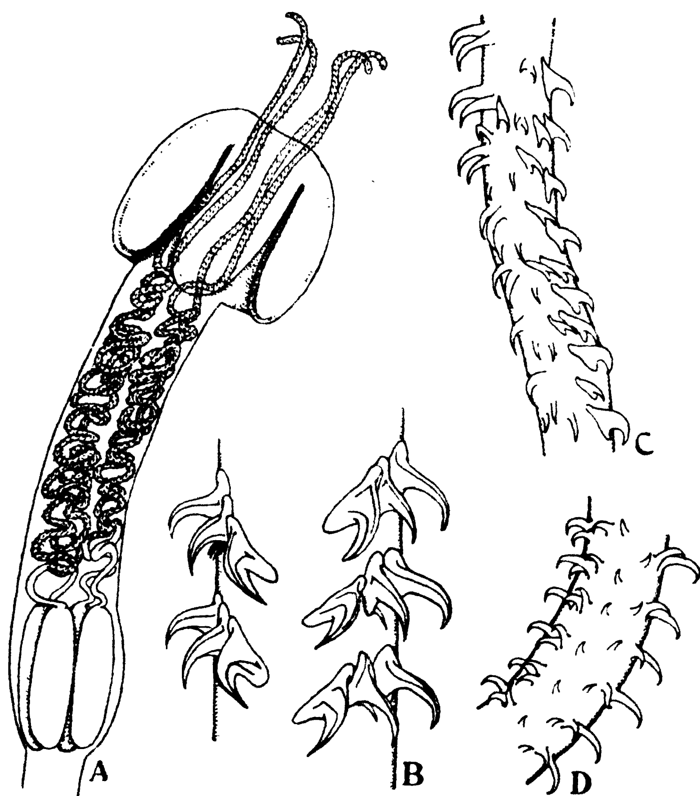


Fig. 19.—*Tetrarhynchus shipleyi*. A, head, ×35; B, proboscis hooks, ×175; C, D, proboscis hooks, ×300. (After Southwell.)

approximately 25 μ and the smallest about 5 μ. That portion of the head between the bothridia and the proboscis sacs measures 2 mm.

Testes and Vas deferens. The testes are very numerous, and fill the entire central field, being densely crowded together. In distribution they present one striking peculiarity in that they

extend posteriorly to the ovary. The cirrus pouch covers two-fifths the breadth of the segment.

The rudiments of the ovary are situated a little distance from the posterior margin of the segment, and, as noted above, a number of testes lie posteriorly to the ovary. No further anatomical details regarding the genitalia could be made out on account of immaturity

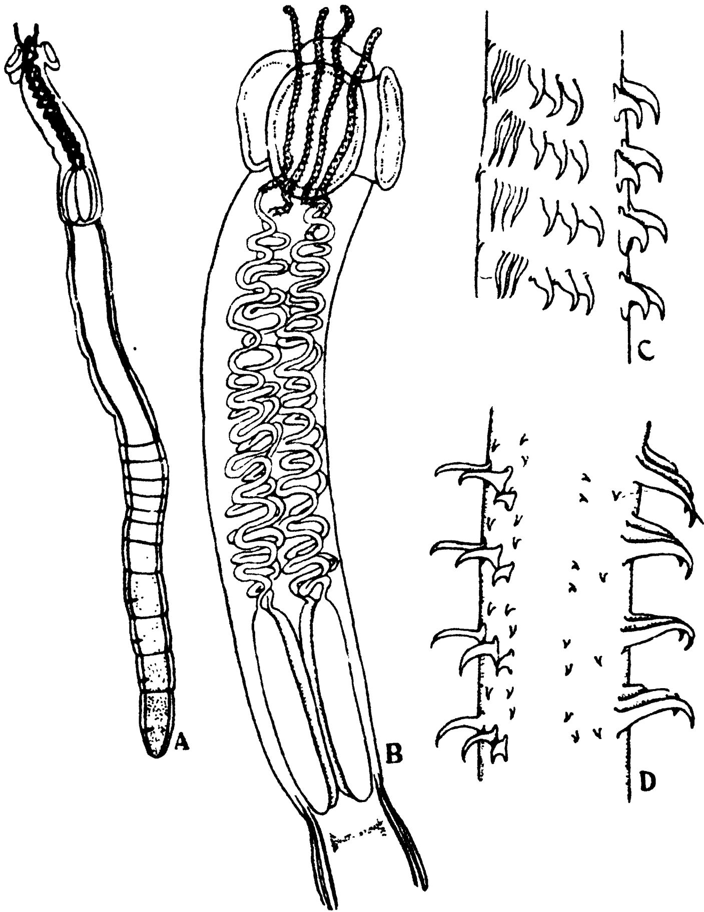


Fig. 20.—*Tetrarhynchus ceylonicus*. A, entire worm, ×9; B. head, ×30; C, D, proboscis hooks, ×400. (After Southwell.)

(5) **Tetrarhynchus ceylonicus** Southwell, 1929. (Fig. 20.)

From *Ginglymostoma concolor*. Pearl Banks, Ceylon. Southwell.

The parasites have a length of 1·5 cm., and the greatest breadth is 900 μ. The neck measures 4 mm. The first segments have a length of over 100 μ and they rapidly elongate; the posterior one is 1·8 mm. It was impossible to count the number of segments exactly, but there were about 14. Rudiments of the very numerous testes could be clearly seen in the last four segments. The genital pore is situated in the posterior lateral half of the segment. The four excretory vessels were prominent.

Head. The head measures 4 mm. in length. Its breadth across the sacs is 770, across the bothridia 900, whilst between the sacs and the bothridia the breadth is 680 μ. The proboscis sacs measure 1·08 mm. in length and the breadth of each sac is 200 μ. They are are thus, roughly, one-fourth the length of the head.

There are four bothridia, each having a length of 630 μ and an approximate breadth of 360 μ. Rows of cilia 13 μ in length run parallel to, and at a distance of 18 μ from, the margin of each bothridium.

Within the head the proboscis tubes are much coiled, and the free portions of the proboscides are short. The hooks are spirally arranged, and are generally large and gross. Their arrangement on the two surfaces of the proboscides is shown in fig. 20. The largest hooks measured 30 and the smallest about 3 μ in length.

(6) **Tetrarhynchus matheri** Southwell, 1929. (Figs. 21 & 22.)

From *Ginglymostoma concolor*, Pearl Banks, Ceylon. Southwell.

Unfortunately in every specimen all the hooks had disappeared from the proboscides. The specimens were almost mature, but not gravid, and a brief account is here given of the anatomy.

The worms measure up to 1·5 cm. in length and the greatest breadth is 500 μ. They are composed of about forty segments with perfectly straight margins, the last one measuring 1 mm. in length and 500 μ in breadth. The genital pores are irregularly alternate, and are situated in the posterior fifth of each segment. The neck is very short, measuring only 160 μ in length.

Head. The head measures about 2·4 mm. in length. The breadth across the bothridia varies according to their state of contraction, but the average is about 750 μ. The breadth of the head in the vicinity of the bulbs is 440 μ, whilst between the bulbs and the bothridia it is 250 μ. There appear to be four bothridia, having a length of 240 and a breadth of about 600 μ; it is quite possible, however, that

there are only two bothridia, each one being almost completely divided into two with a space between the two halves, as in *Tetrarhynchus perideræus*. Their margins are slightly thickened ; a group of cilia runs parallel to the margin at a distance of about 15 μ. The breadth of the ciliated area is about 5 μ, and the cilia themselves measure only 1 or 2 μ.

The proboscis sacs have a length of 550 and a breadth of 140 μ ; there is no collar.

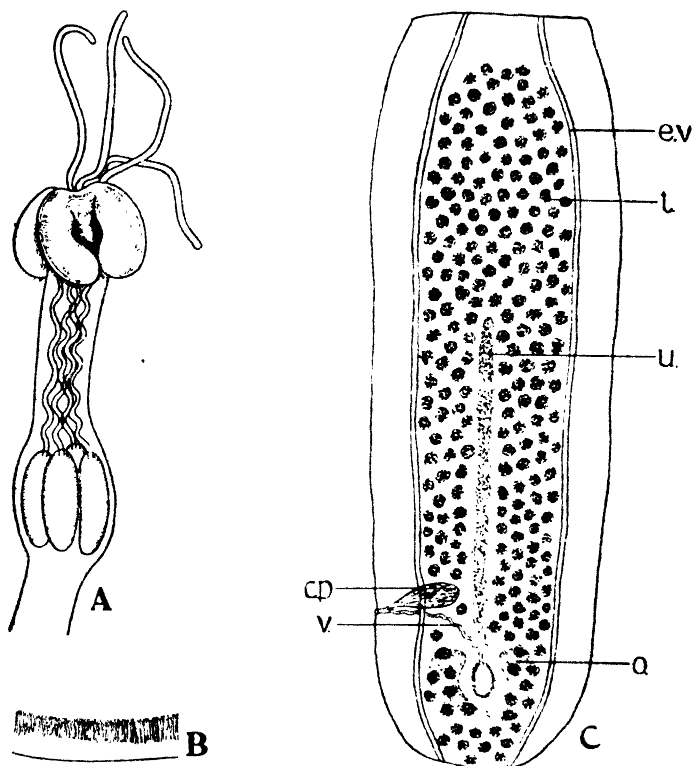


Fig. 21. --*Tetrarhynchus mathert*. A, head, ×46 ; B, margin of bothridium, showing cilia, ×400 ; C, mature segment, ×96. (After Southwell.)

The nervous, muscular, and excretory systems were not investigated, but the two longitudinal excretory vessels on each side were prominent.

Testes and Vas deferens. The twentieth segment is almost square (240 μ), but the testes are not to be seen until the segment becomes much longer than broad. They are very numerous, and occupy the entire central field between the excretory vessels. They extend posteriorly to the ovary on both sides ;

each has a diameter of about 40 μ. The cirrus pouch and vas deferens were not fully developed. The former extends

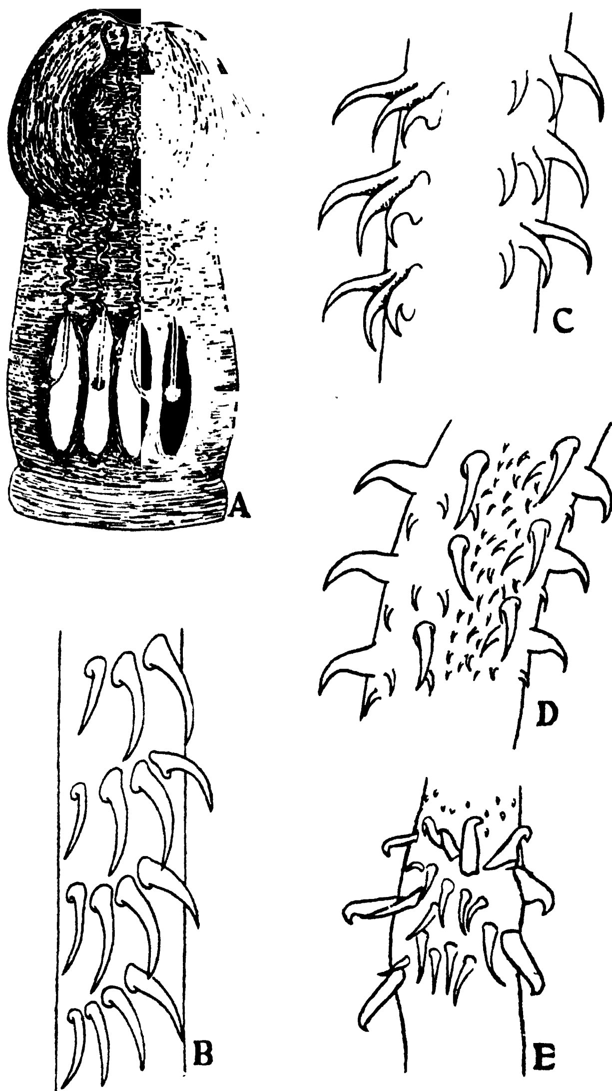


Fig. 22.—*Tetrarhynchus matheri*. A, larva, ×55; B, C, D, proboscis hooks, ×500; E, proboscis hooks, × 400. (After Southwell.)

nearly to the middle of the segment, and the excretory vessel is bent deeply in the vicinity of the pouch.

Ovary. The ovary is situated a little distance from the posterior extremity, and the testes overlie the ovary dorsally and extend posteriorly to it. No details relating to the oviduct, shell gland, or vitelline glands could be ascertained. The uterus was not developed.

The species can be identified by its small size, the position of the genital pore, and by the peculiar appearance of the bothridia.

Numerous larval forms with the bothridia exactly like those of *T. matheri* were obtained from the mesenteries of *Balistes* sp., Pearl Banks, Ceylon. Southwell.

The cysts vary in size; they are cylindrical in shape with rounded extremities, and milky white in appearance. The largest measures 2 cm. by 1·5 mm. The larva measures 1·7 mm. in length and has a maximum breadth of 500 μ. There are four bothridia, exactly similar to those figured for the adult of *T. matheri*. The proboscis sacs have a length of from 500 μ to 540 μ, and the proboscides are fixed near the middle of the proboscis sacs. The larva does not bear a blastocyst posteriorly. Each proboscis is slightly swollen at its base and bears hooks of different shapes from those found over the rest of the proboscides, and many of them are stouter. Moreover, they do not appear to be arranged spirally.

On this basal portion the hooks on one face are straight, slender, with their points slightly enlarged, and they vary in size from 6 to 17 μ. Laterally these are flanked with larger and stouter hooks 30 μ in length, some of which are curved and gradually come to a point, whilst others are stout and have the same diameter throughout except the tip, which is sharply bent at an angle of almost 180°. On the other side of the swollen base of the proboscis there are two longitudinal rows of stout rose-thorn-shaped hooks with broad bases, with a rather long hook which measures 43 μ.

The hooks on the rest of the proboscis are arranged in such a manner that a diagnosis of the species is comparatively easy. On one face the larger hooks, which are curved, are arranged spirally, and there are two or three such hooks in each spiral. They each measure 20 μ. Between these spirals there are irregular numbers of hooks, all small, and of sizes varying from about 5 to 11 μ arranged irregularly, and reminding one of similar hooks in *Tetrarhynchus erinaceus*. These irregularly-disposed small hooks are a continuation of those situated on one face of the swollen base of the proboscis, and they change in numbers, size, and arrangement along its length. On the other face they are large, spirally arranged, curved, measuring from about 20 to 25 μ, and similar to the two or three large ones, also arranged spirally, on the other face of each proboscis.

(*b*) Larval Forms.

(7) **Tetrarhynchus pearsoni** Southwell, 1929. (Fig. 23.)

From *Cybium guttatum*, Pearl Banks, Ceylon, and Puri, Orissa, India. Southwell.

The entire larva consists of a head only, to which no vesicle is attached. It measures from 2·8 to 3·2 mm. in length, and its breadth across the bothridia is 720 μ, the breadth across the r emainder of the head being about 500 μ. There are four

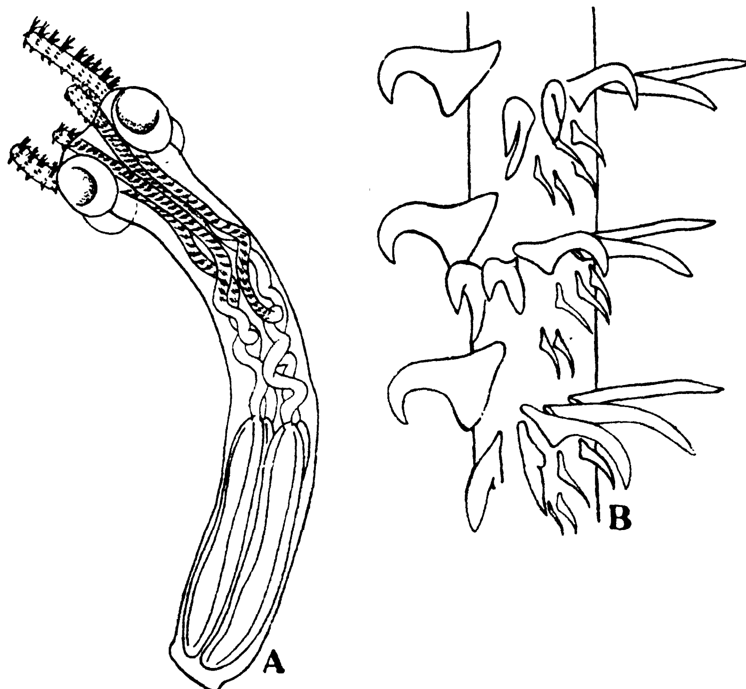


Fig. 23.—*Tetrarhynchus pearsoni*. A, larva, × 27; B, proboscis hooks, × 214. (After Southwell.)

sucker-like bothridia, each having a diameter of 360 μ. The proboscis sacs are practically half the length of the head. Within the head the proboscides are much coiled. They are armed with very distinctive hooks of various shapes and sizes, arranged spirally.

The upper surface (dorsal ?) of each proboscis bears six large hooks in each spiral; a single large rose-thorn-shaped hook is situated along the lateral margin. It has a length of 86 μ and a broad base measuring 64 μ. The succeeding hooks in

each spiral become less and less rose-thorn-shaped and more and more sabre-like until, along the opposite margin, they are very elongated, sabre-like, with small roots, having a length of 105 μ. Between these elongated hooks in each spiral (*i.e.*, along the opposite margin of the proboscides to that bearing the gross rose-thorn-shaped hooks) there are clusters of regularly arranged minute delicate hooks varying in size from 6 to 26 μ (fig. 23). These minute hooks are continued on the other side (ventral ?) of each of the proboscides, whilst on the lateral margin beneath (ventral to ?) the rose-thorn-shaped hooks there are two or three other large spines.

The head bears a general resemblance to that figured by Shipley and Hornell as *Tetrarhynchus rubromaculatus* (Diesing), but the hooks on the proboscides differ. In Shipley and Hornell's figures no rose-thorn-shaped spines are indicated, and the number of small spines shown by these authors are too few. The hooks resemble strongly those of *Tetrarhynchus erinaceus*, but in *T. pearsoni* there are four cup-shaped proboscides, whilst in *T. erinaceus* there are two large flap-like proboscides.

SPECIES INQUIRENDÆ.

(8) **Tetrarhynchus balistidis** Shipley & Hornell, 1904. (Fig. 24.)

From *Balistes stellatus* and *B. mitis*, Pearl Banks, Ceylon. Shipley and Hornell.

"Well advanced metacestoid larva, still retaining the body, 12 mm. to 13 mm. in length. Head triangular, enveloped by a closely wrapping vesicle which leaves the body free. Body crowded with calcareous corpuscles. Teeth of introvert few, only four or six in a transverse row, strongly hooked. Introvert sheaths confined to the head and not entering the body, which it seems is, after a certain time, thrown off with the vesicle. Apparently four lappets. In subperitoneal tissue." (*Shipley & Hornell.*)

(9) **Tetrarhynchus minimus** Linstow, 1904. (Fig. 25.)

From *Tæniura melanospila*, Pearl Banks, Ceylon. Shipley and Hornell.

"Length 3·7 mm.; the last proglottis measures 1·6 mm. in length and 0·39 mm. in breadth. The body consists of about six proglottides. The scolex or head bears on its anterior third four roundish projections directed backwards; these are the proboscis sheaths from which the proboscides are protruded. The projections bear very minute, closely packed hooks; from their apices the proboscides protrude, and these bear larger hooks at wider intervals. There is a regular gradation in the size of the proboscis hooks. The part

of the proboscis which is retracted is arranged in a wavy fashion. The reproductive pore is lateral on the posterior third of each proglottis, but for the most part only immature proglottides were present. The ova are thin-shelled, spherical, with a

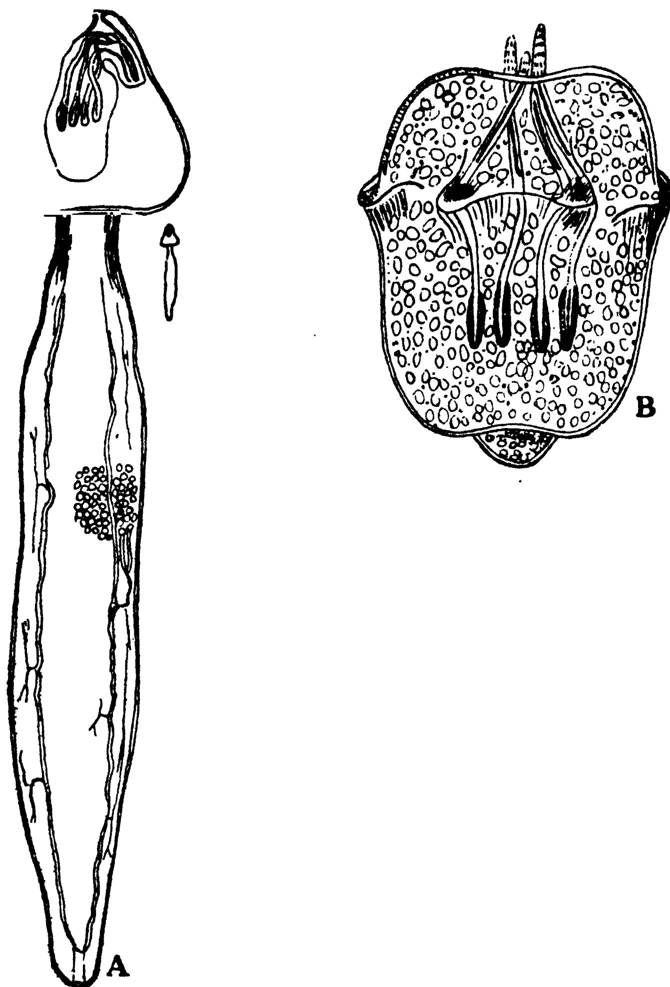


Fig. 24. *Tetrarhynchus balistidis.* A, cyst, × about 10; B, larva, × 12. (After Shipley and Hornell.)

diameter of 0·039 mm. This is the smallest of all species of *Tetrarhynchus*." (*Linstow.*)

The appearance and position of the bothridia and the form and disposition of the hooks on the proboscides in

Linstow's figure leads the writer to believe that this worm belongs to the genus *Gymnorhynchus*, and probably to the species *gigas*.

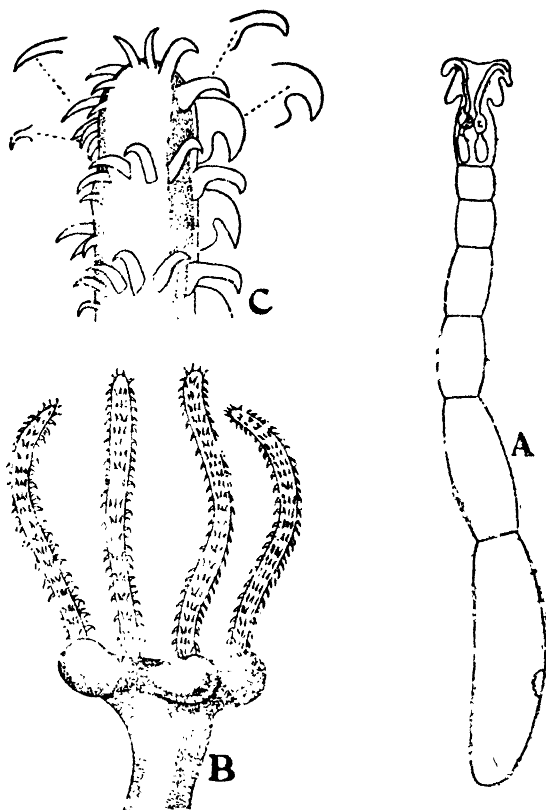


Fig. 25.—*Tetrarhynchus minimus*. A, entire worm; B, head; C, proboscis hooks. Magnification unknown. (After Linstow.)

(10) **Tetrarhynchus** sp. Shipley & Hornell, 1906. (Fig. 26.)

From *Balistes mitis*, Pearl Banks, Ceylon. Shipley and Hornell.

" Like *T. balistidis*, and consists of a head which has not yet begun to bud off proglottides. The anterior part of the head bearing the lappets is just about as long as the part bearing the proboscis sacs, whilst the median portion traversed by the proboscis sheaths is two or three times as long as either. The proboscis teeth are graded in each row from long, narrow,

sabre-like outlines to short beaked forms. From the account drawn up at the time of capture from the living material this

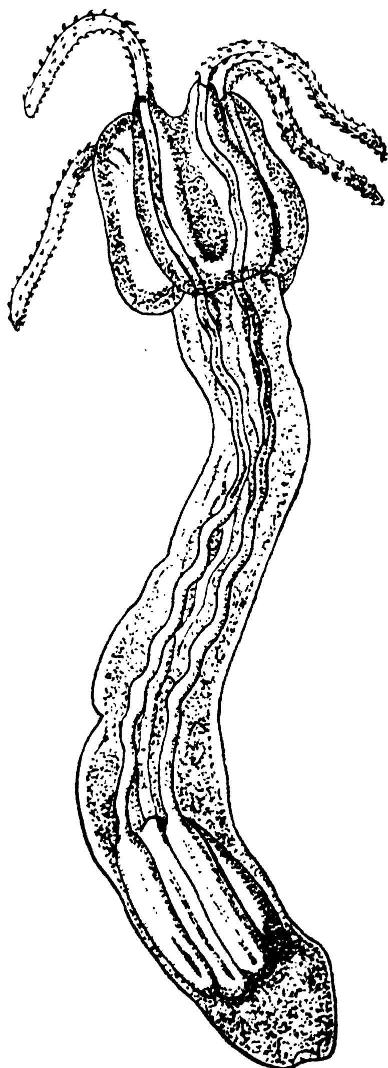


Fig. 26.—*Tetrarhynchus* sp. From *Balistes mitis*, × 40. (After Shipley and Hornell.)

form had evidently only just escaped from a cyst of the *T. erinaceus* type. (*Shipley & Hornell.*)

It is impossible to identify this larva.

Genus II. TENTACULARIA Bosc, 1797.

Small to medium-sized worms; head with two bothridia lying parallel to the body and having the sucking surfaces facing externally, each of which may be simply emarginate or partly divided longitudinally into two.

Type-species :—*Tentacularia coryphænæ* Bosc, 1802.

As the principal differences between the 16 adult species dealt with below have reference to the size and shape of the hooks on the proboscides, it is not possible to provide a key.

(a) Adult Forms.

(1) Tentacularia minuta (van Beneden, 1849). (Fig. 27.)

Synonym :—*Tetrarhynchus minutus* van Ben., 1849.

From *Carcharias* sp. and *Rhina halavi*, Negapatam, India; and from *Carcharias* sp., Pearl Banks, Ceylon. Pearson.

This is the first report of this parasite in Ceylon. It has been recorded previously from *Squatina angelicus* and *Urolophus testaceus* in Europe.

The worm measures about 4 mm. in length and the greatest breadth (in a gravid segment) is 330 μ; it is composed of from three to six segments, usually three or four, the last being longer than the rest of the worm and measuring 2·25 mm. in length and 270 μ in breadth. The genital pore is situated in the posterior quarter of the segment. There is no neck.

Head. The head has a length of 1·2 mm.; its breadth across the bothridia is 400 μ, whilst in the vicinity of the proboscis sacs the breadth is 220 μ. There are two sucker-like bothridia, each having a diameter of 140 μ.

The proboscis sacs are a little more than half the length of the entire head. They vary slightly in size and, when the head is contracted, they occasionally extend anteriorly almost to the bothridia. They have a length of 630 μ and a breadth of 65 μ. The proboscides are much coiled within the head, and their free portions are quite as long as the head.

The arrangement and form of the hooks on the proboscides is shown in fig. 27.

The base of each of the proboscides is swollen and armed with peculiar hooks. This arrangement of the hooks is slightly different from that figured by Scott (1907) for this species. This is possibly due to the fact that Scott, owing to the low magnification used by him, confused the hooks on the dorsal surface with those on the ventral surface.

The nervous, muscular, and excretory systems were not investigated.

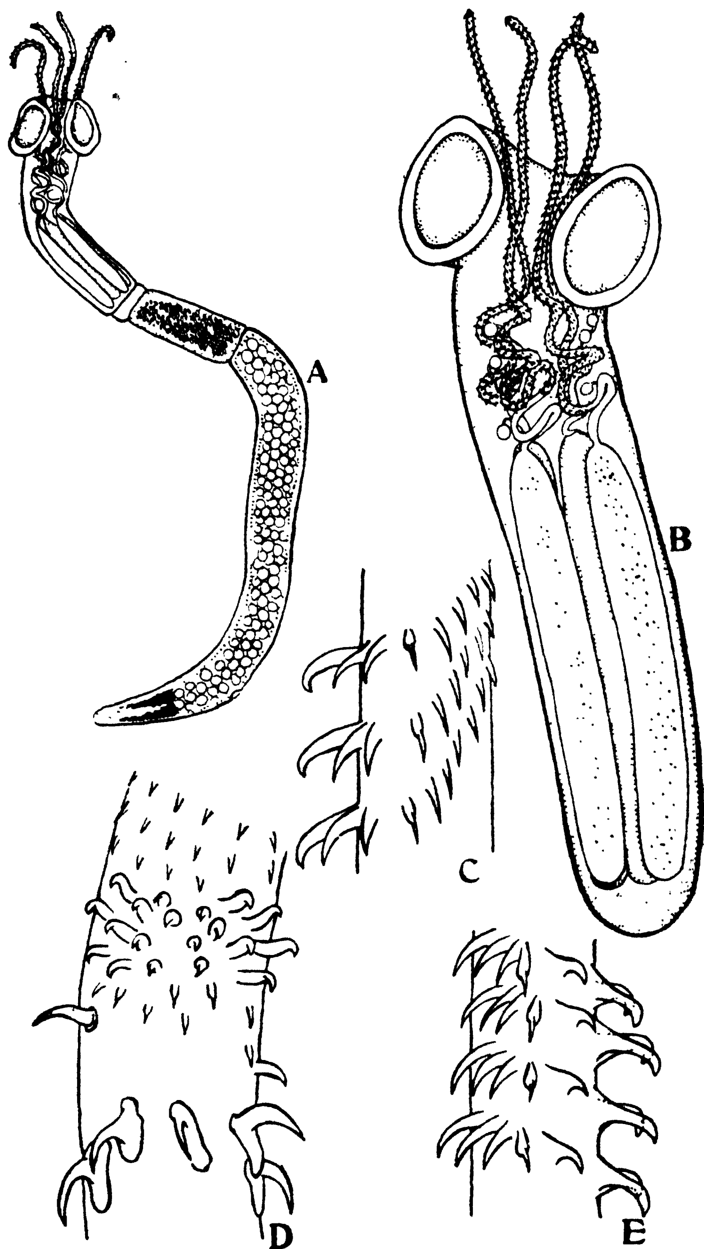


Fig. 27.—*Tentacularia minuta.* A, entire worm, × 26; B, larva, × 290; C, D, hooks from middle of proboscis, × 750; E, basal hooks, × 750. (After Southwell.)

Testes and Vas deferens. The testes are very numerous and fill the entire field anterior to the ovary. The cirrus pouch and vas deferens could not be seen in whole mounts on account of the fact that they were hidden, as was the vagina, by the testes and the vitelline glands.

Ovary. This is situated posteriorly, each lobe being elongated and apposed to the wall of the segment.

Vitelline Glands. These encircle the segment, but are developed most fully along the lateral margins.

Uterus. This is a simple wide sac entirely filling the segment.

As the species bears two bothridia only, it is referred to the genus *Tentacularia*.

In 1904 Linstow described a new species (*Tetrarhynchus minimus*) from the spiral valve of *Tæniura melanospila* caught in Ceylon. Whilst agreeing in dimensions with *T. minutus* (van Beneden, 1849), it differs from it in the following points :— in having four bothridia, in the shape of the hooks, and in the relative length of the bothridia.

The head shown by Linstow in his fig. 70 suggests that his species belongs to the genus *Gymnobothrium*.

(2) **Tentacularia longispina** (Linton, 1890). (Fig. 28.)

Synonym :—*Rhynchobothrium longispine* Linton, 1890.

From *Dasybatus walga*, Pearl Banks, Ceylon. Southwell.

One specimen of what the writer believes to be this species was obtained from the above host.

The worm, which is composed of about seven segments, measures 6 mm. in length, and the maximum breadth is 290 μ. The last segment measures 2·5 mm. in length and 290 μ in breadth.

The head measures 1·3 mm. in length ; its breadth across the bothridia is 400, across the proboscis sacs 300, and between the bothridia and the sacs 280 μ. There are two simple small bothridia having a length of 200 μ.

Only the terminal portions of the proboscis were protruded, and the hooks resembled those figured for this species by Linton in size and appearance.

(3) **Tentacularia macrocephala** (Shipley & Hornell, 1906). (Figs. 29 & 30.)

Synonyms :— *Tetrarhynchus macrocephalus* Shipley & Hornell, 1906.
Tetrarhynchus ruficollis Shipley & Hornell, 1906 (not Eysenh., 1829).

From (1) *Dasybatus walga*, Pearl Banks, Ceylon. Shipley and Hornell. (2) *Rhynchobatus djiddensis*, *Dasybatus kuhli*, and *D. walga*, Pearl Banks. Ceylon. Southwell.

Shipley and Hornell described this worm as follows:—"At least six different species of *Tetrarhynchus* are found in the intestine of *Trygon walga*. This species is a short, stout,

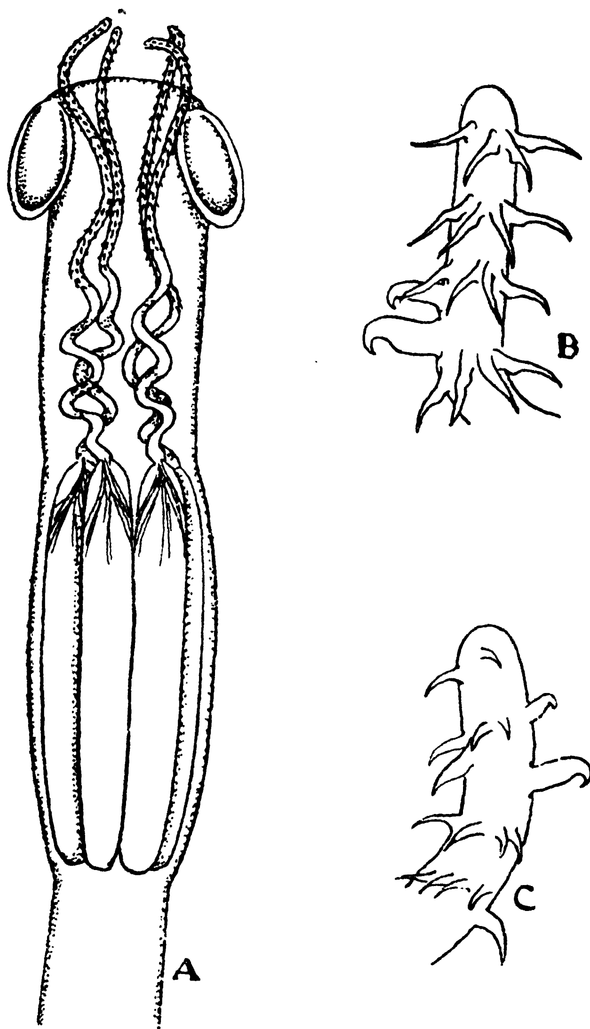


Fig. 28.—*Tentacularia longispina*. A, head and neck, × 40; B, C, proboscis hooks, × 320. (After Southwell.)

thick-set form, with large bothridia or lappets which, however, when the proboscides are extended are far less conspicuous than when they are retracted.

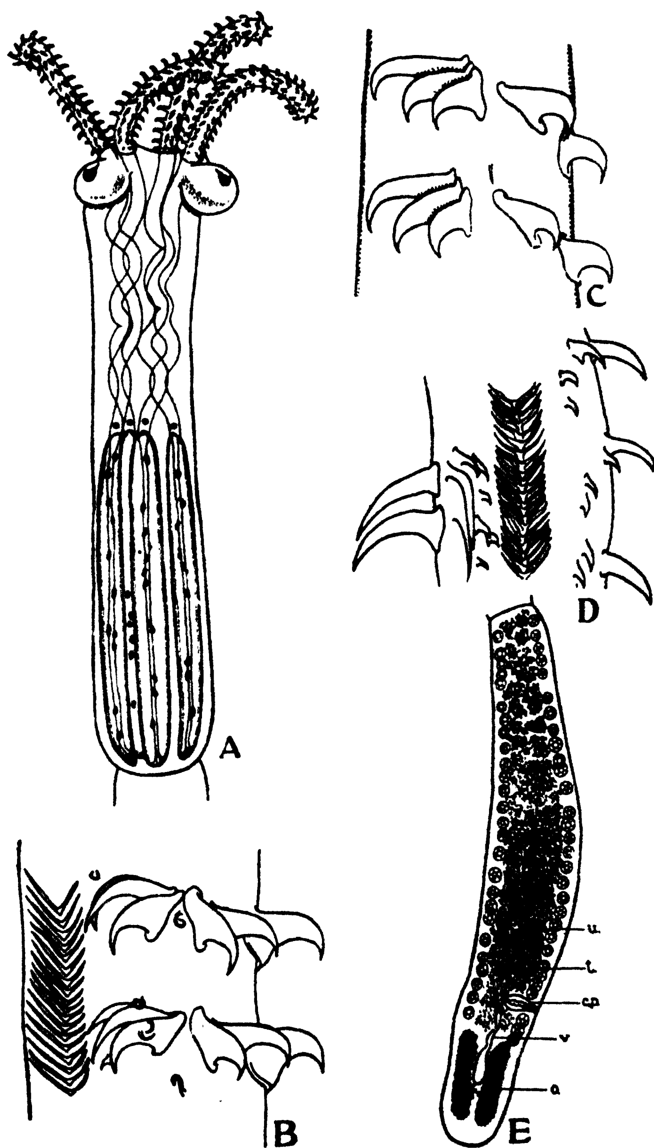


Fig. 29.—*Tentacularia macrocephala.* A, head, × 17; B, C, proboscis hooks, × 175; D, proboscis hooks, × 150; E, nearly gravid segment, × 19. (After Southwell.)

"The total body length averages 7 mm. or 8 mm., and the body is stiff and straight. The relative length of the different parts of the body in one specimen whose total length was 8 mm. was 3 mm. for the part of the head traversed by the coiling ducts of the proboscis sheath, 3 mm. for the part of the head which contains the muscular proboscis sheath, and 2 mm. for the rest of the body. The second portion, that which contains the muscular sheath, is the thickest, and its walls are smooth; the anterior half of the head is wrinkled.

"The four proboscides were in some specimens extended, but not fully; they attained a length of some 2 mm. Each bears a longitudinal double row of minute, almost straight spines, diverging from one another, the whole producing the effect of a stitch known, I believe, to housewives as 'herring-boning.' This lies the whole length of the proboscis. There are also very numerous sharply hooked spines which lie in transverse rows of some hundred or more in number. Each of these rows consists of some ten or twelve hooks, grading in size from the largest, which is just opposite the 'herring-boning,' to the smallest, which flank the 'herring-boning.'

"When the whole is retracted it passes first into the very coiled ducts of the muscular sheaths, which are very apparent in the specimen.

"The strobila is smaller than either half of the head; the piece immediately succeeding the head is anteriorly concave, and receives into its concavity the convex end of the head. It soon begins to 'segment,' and the proglottides grow rapidly. They are few in number, and the most posterior, which is about the tenth or twelfth, is almost as large as all the others put together. It shows clearly the exit of the water vascular system. The specimens were probably young ones."

A more detailed account of the anatomy is now given.

The worms measure up to 5 cm. in length, and the maximum breadth of the strobila is about 650 μ. It is composed of about 30 to 35 segments, the last one (gravid) measuring 4 mm. in length and 650 μ in breadth. The genital pores are irregularly alternate and situated in the posterior fourth of the segments. There is no neck.

Head. The head measures from 7 to 8 mm. in length; its breadth across the bothridia is about 1·3 mm., across the proboscis sacs 750 μ, and between them and the bothridia 600 μ. There are two sucker-like bothridia having a diameter of about 600 μ. The proboscis sacs have a length of 2 mm. and a breadth of about 270 μ. They are marked by fine criss-cross lines. The proboscides can be seen running to the posterior extremity of the sacs, and along their course, within the sacs, they bear numerous coarse granules, each having a diameter of about 40 to 60 μ. A single granule is

also usually present at the exit of each of the proboscides from its sac. The hooks on the proboscides are of various shapes and sizes, but most of them are large and gross. First, on each of the proboscides there is a conspicuous herring-bone pattern,

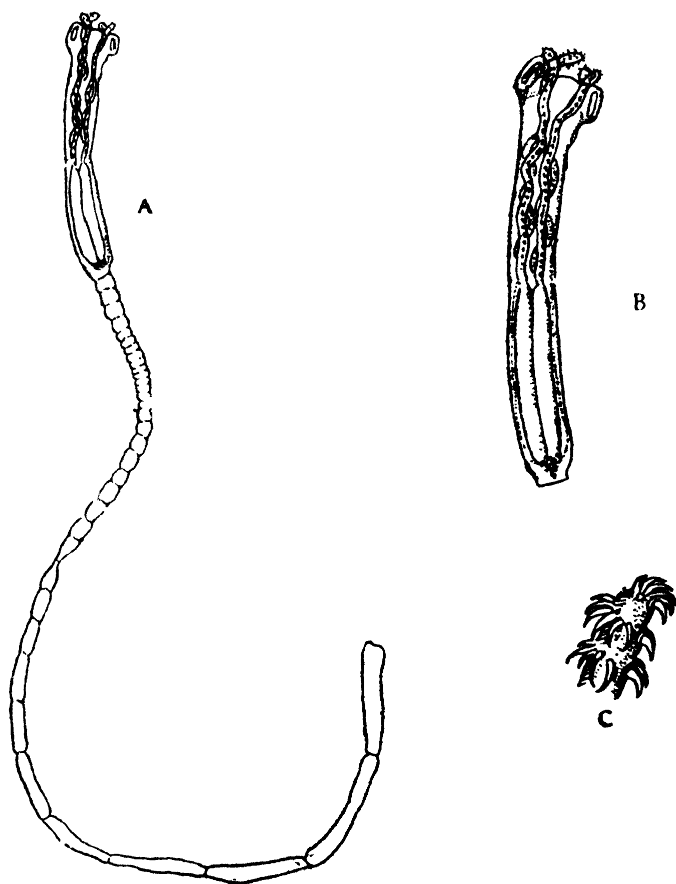


Fig. 30.—*Tentacularia macrocephala.* A, entire worm, × 6; B, head, × 12; C, proboscis hooks. Magnification unknown. (After Shipley and Hornell.)

or marking, running the whole length of the proboscides, and this pattern is not composed of hooks, but of markings on the surface of the proboscides; the largest measure over 70 and the smallest 2 or 3 μ.

The nervous, muscular, and excretory systems were not investigated.

Testes and Vas deferens. There are about 60 testes and they fill the entire segment, extending posteriorly, on both sides, to the ovary. Each testis has a diameter of about 80 μ. The cirrus pouch extends to the longitudinal axis, and the cirrus is unarmed.

Ovary and Vagina. The ovary is bilobed and posterior, each lobe being apposed to the wall of the segment, and consisting of 15 or 16 large acini. The vagina is short.

Vitelline Glands. The vitelline glands encircle the entire segment, but the lateral acini are most strongly developed.

Uterus. The uterus is a simple bag entirely filling the segment. The uterine eggs measure about 50 μ ; they are globular, and are devoid of filaments.

Pintner, who examined the type-species, states that *T. macrocephala* Shipley & Hornell is the same as the mature worm, measuring 4 to 5 cm., identified by Shipley and Hornell as *T. ruficollis* (Eysenhardt, 1829), and he further states that the worm identified by Shipley and Hornell as *T. ruficollis* (Eysen.) is quite a different species from that described by Eysenhardt.

The species is easy to identify on account of (1) the very large head, bearing two small bothridia ; (2) the presence on one side of each of the proboscides of a "coat of mail or armoured chain" or herring-bone pattern ; (3) the coarse granules scattered irregularly on the proboscides within the proboscis sacs.

Shipley and Hornell described their "*T. ruficollis*" as follows :—"Several specimens of this worm were taken from the intestine of *Trygon walga*. They measure 40 mm. to 50 mm. and had the characteristic criss-crossing of the proboscis sheaths. The teeth are not quite so regular as in van Beneden's specimens, and he does not figure any of the posterior proglottides ; these are cylindrical and smooth, the same diameter throughout, and eight to ten times as long as they are broad. They are so cylindrical that it is impossible to say whether the genital pore is on the edge or median. There are besides the larger teeth arranged in more or less oblique rows, two longitudinal chains of very minute tubercles. Van Beneden's specimens came from *Mustelus vulgaris* Müll. & Henle, ours came from the intestine of *Trygon walga* Müll. & Henle."

Pintner (1913) considers that *T. ruficollis* Shipley & Hornell, 1906 (not Eysenh., 1829), is synonymous with *T. macrocephala* (Shipley & Hornell, 1906). On account of the peculiar arrangement of the hooks on the proboscis in the latter species Pintner places the worm in his new genus *Halysiorhynchus*,

calling the type-species *H. shipleyanus* (=*T. macrocephala* Shipley & Hornell, 1906).

The identity of the parasite named *T. ruficollis* by Shipley and Hornell is doubtful.

(4) **Tentacularia macropora** (Shipley & Hornell, 1906). (Figs. 31 & 32.)

Synonyms :—*Tetrarhynchus macroporus* Shipley & Hornell, 1906.
Tetrarhynchus annandalei Hornell, 1912.

From (1) *Dasybatus uarnak*, Pearl Banks, Ceylon. Shipley and Hornell. (2) *Stegostoma tigrinum*, Bay of Bengal. Hornell. (3) *Galeocerdo arcticus*, *S. tigrinum*, and *Dasybatus* sp., Pearl Banks, Ceylon. Pearson.

Shipley and Hornell described this parasite as follows :—
"These are fair-sized Tetrarhynchids, averaging about 25 mm. in length and 1 mm. in breadth.

"The lateral lappets are small, each divided into two, each half corresponding with one of the four hooked proboscides. The head is 6 mm. long and swells out a little behind where the muscular sheaths of the proboscides lie. When alive, there is a patch of pink anterior to these sheaths. Each proboscis bears on its concave side, when unrolled, a number of strongly recurved teeth which gradually pass into a much straighter, sabre-like tooth on the convex side. The recurved teeth have a marked anterior process, something like a sword-guard where the tooth passes into the haft, which is embedded in the tissue. This is absent in the more sabre-like teeth. The teeth are in rings which are obliquely placed.

"There is practically no neck and the number of the proglottides is small, some 30 to 35. Until the last three or four, the sides of the proglottides are parallel, straight at their ends, and with no sign of overlapping. The whole body is marked by a curious longitudinal striation, which is due to the presence of minute pigment spots and to the fact that these little brownish particles are arranged along certain longitudinal lines ; also these pigment spots seem broken up into other areas, which give a mottled appearance to the skin.

"The last four or five proglottides are remarkable for the enormous development of the genital pore, which sometimes occupies one-quarter to one-third of the length of the proglottis. From this gaping cavity a minute penis protrudes. These same four or five proglottides lose their uniform shape and become very irregular in outline. The pores are in all cases lateral and irregularly alternate."

As the anatomy of this species has not hitherto been described, the writer gives the following account :—

The worm measures up to 6 cm. in length and the greatest

breadth is 1·1 mm. There are over 50 segments, the last one measuring 4·5 mm. in length and 1·1 mm. in breadth. The genital pores are irregularly alternate, and are situated in the posterior half of the proglottid. In the fully mature

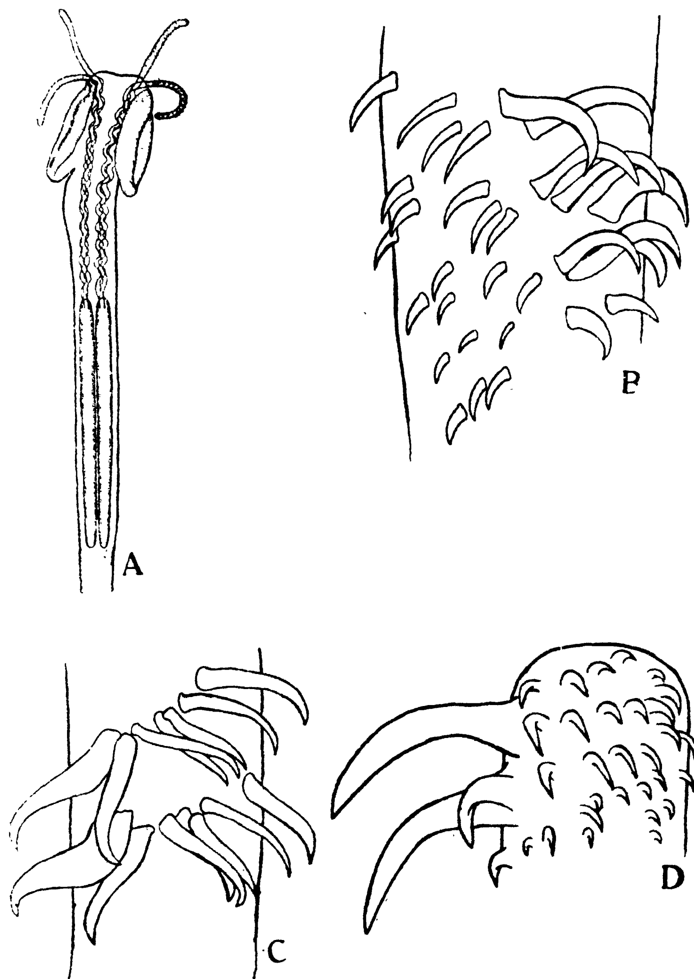


Fig. 31.—*Tentacularia macropora.* A, head, × 7; B, C, D, proboscis hooks, × 160. (After Southwell.)

segment the pore is enormous, and measures 700 μ in length; this is a very striking character. There is a short neck measuring 1·8 mm. in length. Details of the nervous and excretory systems were not investigated.

Head. The head measures 9·4 mm. in length and 1 mm. in breadth ; in the vicinity of the bothridia the breadth is 2 mm. The proboscis sacs measure 5 mm. in length and 400 μ in breadth. There are two very large bothridia, each having a length of 2·2 mm. Posteriorly they are slightly indented. The hooks on the proboscides are not arranged in a definite spiral, and they do not extend far backwards on the proboscides.

The muscular system consists of a large number of small scattered fibres situated externally to the vitelline glands.

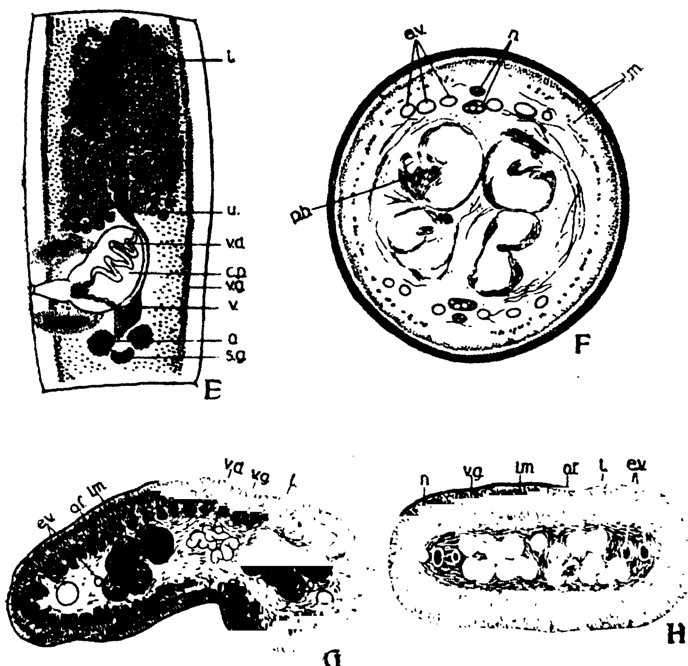


Fig. 32.—*Tentacularia macropora.* E, mature segment, × 18 ; F, transverse section through head, × 56 ; G, transverse section of mature segment, × 56 ; H, transverse section of nearly mature segment, × 56. (After Southwell.)

Testes. The testes are numerous and, when fully developed, each has a diameter of about 70 μ. They are all situated anteriorly to the cirrus pouch. When fully mature they are entirely obscured by the dense vitelline glands which encircle the segment, except at the anterior extremity of the segment.

Vas deferens. The cirrus pouch is an extremely large and conspicuous structure extending beyond the median longitudinal axis of the segment and displacing the rudiment of

the uterus at that point. It measures about 700 μ in length by 500 μ in breadth. Within the pouch the vas deferens presents a striking appearance in being coiled and irregularly dilated, whilst outside the pouch it is equally characteristic in being coiled and extending posteriorly towards the ovary. No external seminal vesicle was noted. Marginally, on each side of the pouch, there is a clear space filled with granular material (glands ?).

Ovary and Vagina. The ovary is typically bilobed and prominent. The vagina is short and strongly coiled. Its opening to the exterior could not be seen in total mounts as its terminal portion was obscured by the cirrus pouch.

Vitelline Glands. These appear late, and eventually encircle the segment entirely, thus obscuring the testes; they are strongly developed and prominent.

Shell Gland. This lies posteriorly to the ovary, and is equal in size to one wing of the ovary.

Uterus. The rudiment of this organ extends in the median antero-posterior longitudinal axis. It is bent aporally in the vicinity of the cirrus pouch because the latter organ extends beyond the median longitudinal axis. No eggs were seen.

The head of *T. macropora* (Shipley & Hornell, 1906) resembles that of *T. ruficollis* Eysenhardt, 1829 (=*T. longicollis* van Beneden, 1849), very strongly. Amongst other points the former species differs from the latter in the possession of an enormous genital pore and cirrus pouch. It should be noted that the appearance of the genital pore varies with the degree of development and with the state of contraction of the segment.

Hornell's description of *T. annandalei* was as follows:—

"Length 3·6 cm. Head cylindrical and fairly long, about 8 mm. Bothridia two, lateral, longer than broad, slightly emarginate on the posterior edge, and with a raised and thickened margin. Proboscides four, long, and strongly armed with curved hooks, the majority long and sabre-shaped, fairly stout; a small number of very minute recurved forms with elongated base present.

"The proboscis sheaths long and arranged in closely-set spirals; this region of the head, including with it the part overlaid by the bothridia, is about equal in length to the posterior section containing the contractile sacs. *The latter region is characteristically of great relative elongation*, and is slightly wider than the anterior head region. The sacs are cylindrical, with the oblique decussation of the muscle fibres well marked. Neck short, one and a half times as long as wide; greatest breadth seen in this worm occurs in the anterior part, which increases in width abruptly immediately behind the contractile sacs. Neck wrinkled slightly transversely.

"Proglottides about 25. Anteriorly they are wider than long, but soon become square and then rapidly elongate, and in the maturing ones the length is twice the breadth. The lateral margins parallel, and none of the proglottides overlap. Cuticle sometimes faintly ringed, but this may be a *vost mortem* effect.

"Last five or six proglottides remarkable for enormous development and prominence of the genital pore. This is lateral, and situated at beginning of posterior third of the marginal length of each proglottis. Position of the pores are alternate in consecutive groups, usually in alternate series 3, *e. g.*, right 1, left 3, right 3."

Hornell pointed out that his species differed from *T. macroporus* in that the bothridia are simple and entire in the former, whereas in the latter species each is divided into halves. Shipley and Hornell, however, state that in *T. macroporus* each bothridium is divided into two. In our specimens of this species, whilst the majority of the bothridia are simple, as figured by Hornell, in a few they are contracted in such a way that, superficially, each bothridium appears to be, but is not, divided.

Southwell (1924) identified a tetrarhynchid from *Dasybatus* sp. as *Rhynchobothrius erinaceus* (van Ben., 1858), and gave *R. imparispine* Linton, 1890, *R. simile* Linton, 1909, *T. gangeticus* Shipley & Hornell, 1912, and *T. annandalei* Hornell, 1912, as synonyms of *T. erinaceus*. Further investigation, and the examination of a much greater amount of material, has shown conclusively that the writer was in error on this point. The specimens named *R. erinaceus* (van Beneden, 1858) proved to be specimens of *T. macroporus* Shipley & Hornell, 1906 (=*T. annandalei* Hornell, 1912), the latter differing from the former in the shape of the hooks and in the size of the cirrus pouch.

R. imparispine Linton, 1890, *R. simile* Linton, 1909, and *T. gangeticus* Shipley & Hornell, 1906, are closely related to but distinct from both *T. erinaceus* van Beneden, 1858, and *T. macroporus* Shipley & Hornell, 1906.

(5) **Tentacularia ætobatidis** (Shipley & Hornell, 1906). (Fig. 33.)

Synonym :—*Tetrarhynchus ætobatidis* Shipley & Hornell, 1906.

From *Stoasodon narinari*, Pearl Banks, Ceylon. Shipley and Hornell.

"This species, of which we had but two specimens, measures 12 mm. in length. The head is squarish, with two well-marked suckers on each side, and the proboscides emerging at the four angles of the anterior surface. These proboscides are perhaps a little stouter and thicker than usual. They bear the hooks

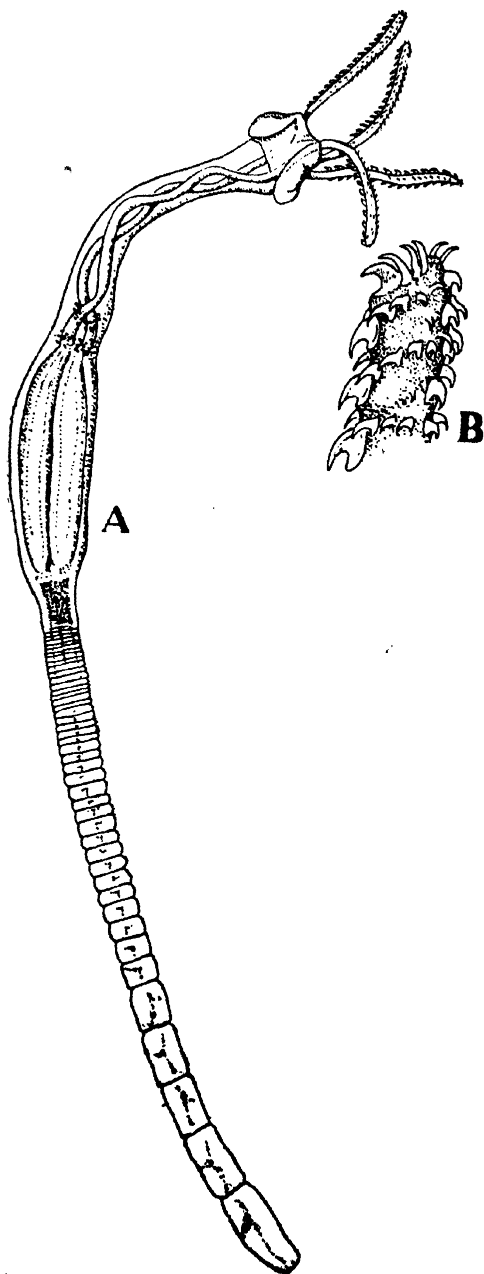


Fig. 33.—*Tentacularia ætobatidis.* A, entire worm, × 12; B, proboscis hooks, × 100. (After Shipley and Hornell.)

in oblique rows. The hooks at the anterior end of the extended proboscides are strongly curved backwards and have a very characteristic haft. There is a prominent projection anteriorly, just where the hook is inserted into the skin. Posteriorly the hooks become more sabre-like.

"One characteristic feature of this species is the swelling which takes place at the posterior half of the head, caused by the presence of the stout muscular bulbs of the proboscis. Just before the junction of the proboscis tubes with the proboscis bulbs are two aggregations of red pigment spots. This region is at least twice the diameter of the succeeding body. There is a short neck, or at least a region where no divisions are visible. The number of the proglottides in our two specimens hardly surpassed thirty-five, but the posterior ones were not mature. The proglottides are barrel-shaped. The reproductive pores are irregularly alternate, but as a rule there are not more than two consecutively on the same side. The cuticle is roughly ringed." (*Shipley & Hornell.*)

They figure this species as possessing two bothridia.

(6) **Tentacularia rhynchobatidis** (Shipley & Hornell, 1906). (Fig. 34.)

Synonym :—*Tetrarhynchus rhynchobatidis* Shipley & Hornell, 1906.

From *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Shipley and Hornell.

"The largest specimen of this *Tetrarhynchus* attained a length of 5 cm.; but, since some loose proglottides measured 4 mm. each, probably the full length is greater and its posterior end a width of 1 mm. The length of the head is 4 mm. The lappets are short and widely separated; anteriorly they occupy 1 mm., and the remaining 4 mm. are divided equally between the part of the head which contains the proboscis tubes and the part which contains the proboscis bulbs. The part of the head which bears the lappets is 1·2 mm. broad, but behind this the head tapers. The colour of the living specimens is an opaque milk-white.

"The hooks in the proboscides are arranged in longitudinal rows and also in rings. The latter are almost horizontal, there being only a very slight trace of obliquity as they surround the stem. One peculiarity, which we have not noticed in other species, is that on each proboscis there is a longitudinal row of hooks whose points are reversed and look towards the tip of the proboscis and not to the base, as do all the others. Some of them are not nearly so hooked as others that pass into sabre-like forms.

"Another peculiarity is that the outer muscles of the proboscis bulb are very oblique, very clear, and cross one another at right angles, giving a 'Malvolio, cross-gartered' appearance to these structures.

"There is a short neck and then a number of proglottides, five or six times as broad as long, separated one from another by perfectly straight lines, and with at first parallel straight sides. They soon, however, begin to lengthen, and at the end of the first quarter they are square. The sides also begin to bow outwards, but the ends are always flat, and there is absolutely no overlapping.

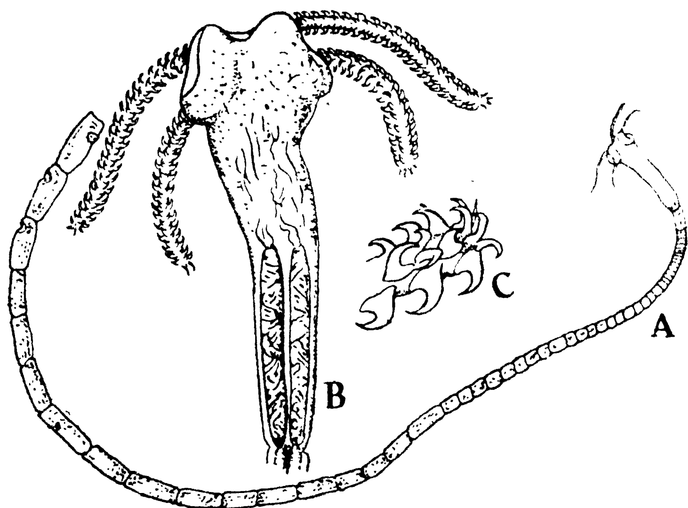


Fig. 34.—*Tentacularia rhynchobatidis*. A, entire worm, × 4 ; B, head, × about 18 ; C, proboscis hooks, × 100. (After Shipley and Hornell.)

"The reproductive pores are lateral, and at the junction of the anterior two-thirds with the posterior third. Their circular lips are prominent and everted. The pores are irregularly alternate ; for instance, starting at the last of one specimen, they run as follows :—1 right, 3 left, 2 right, 1 left, 1 right, 2 left, and so on." (*Shipley & Hornell.*)

It is possible that this parasite may be recognizable on account of the longitudinal row of reversed hooks on each of the four proboscides. The worm described by the writer under this name in 1924 has since proved to be a new species which has been named *R. johnstonei*. Shipley and Hornell's figure of the species shows the head bearing two bothridia.

? Tentacularia rhynchobatidis (Shipley & Hornell, 1906).

From *Balistes mitis*, Pearl Banks, Ceylon. Pearson.

The cyst has the form and appearance of that containing *Otobothrium dipsacum*, but it differs from it in the following points :—

(*a*) The colour is light brown and the outer cyst wall is stout but very friable, with a mosaic of rounded light brown markings.

(*b*) The larvæ are attached to the side of the cyst near the middle.

The larval head is very large, measuring 5 mm. in length, and the two bothridia each measure 1·5 mm. A line of cilia runs parallel to their margins, but disappears anteriorly. The writer has not seen the adult worm. In the larval form the proboscides were not protruded ; the characteristic feature of this species is the fact that on each proboscis there is a longitudinal row of hooks whose points are reversed and look towards the tip, and this could be seen even in the invaginated proboscides.

(7) **Tentacularia gangetica** (Shipley & Hornell, 1906). (Fig. 35.)

Synonym :—*Tetrarhynchus gangeticus* Shipley & Hornell, 1906.

From *Carcharias gangeticus*, Pearl Banks, Ceylon. Shipley and Hornell.

Worms 10 mm. in length, 2 mm. in breadth, and the head is 3 mm. at least in width. It "has a smooth white head, two very clearly defined and large lappets, somewhat heart-shaped, the apex pointing forward and the four proboscides issuing near the two apices, two on each side. The proboscides are stout and bear teeth of many sizes. On the concave side of the extruded proboscis are large, strongly recurved teeth ; these are flanked by teeth of lesser size, and they gradually diminish until upon the convex side there are a multitude of fine toothlets ; although it is rather masked, these teeth are really arranged in very obliquely placed rings.

"The edges of the lappets are outstanding and sharply separated from the head, and they have clear-cut edges.

"The proboscis-tubes leading to the proboscis-bulbs are not spirally twisted so much as bent in and out. The head narrows posteriorly ; anteriorly it is 2 mm. in width, and the whole is 3 mm. in length.

"There is no neck ; the proglottides appear immediately after the head. As there were but three specimens, one only was mounted, and this shows only just the anterior five or so proglottides." (*Shipley & Hornell.*)

Pintner (1913) places this species along with *T. herdmani* Shipley & Hornell, 1906, *T. perideræus* Shipley & Hornell, 1906, *T. lingualis* (Cuvier, 1817), *T. bisulcatus* Linton, 1889, *T. robustus* Linton, 1890, *T. tenuis* Linton, 1890, and also *T. macrobothrius* Rud., 1819, in his genus *Stenobothrium*.

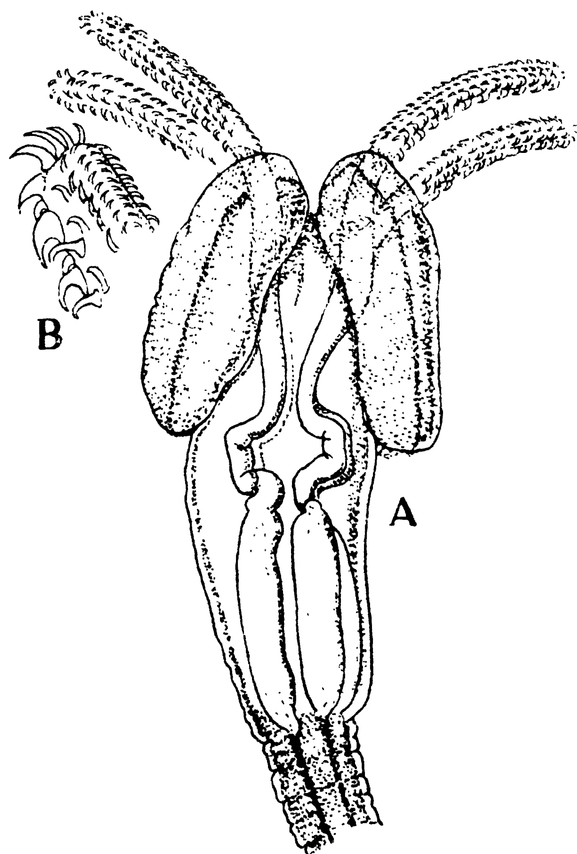


Fig. 35.—*Tentacularia gangetica*. A, head, × 20 ; B, proboscis hooks, magnification unknown. (After Shipley and Hornell.)

T. gangeticus is, however, very different from the species named above, especially in the absence of a collar and in the hooks being of different shapes and sizes.

Linton (1924) has recorded the larval form from the muscles of *Sciæna hololepidota*, Mossel Bay, South Africa.

(8) **Tentacularia carcharidis** (Shipley & Hornell, 1906). (Fig. 36.)

Synonym:—*Tetrarhynchus carcharidis* Shipley & Hornell, 1906.

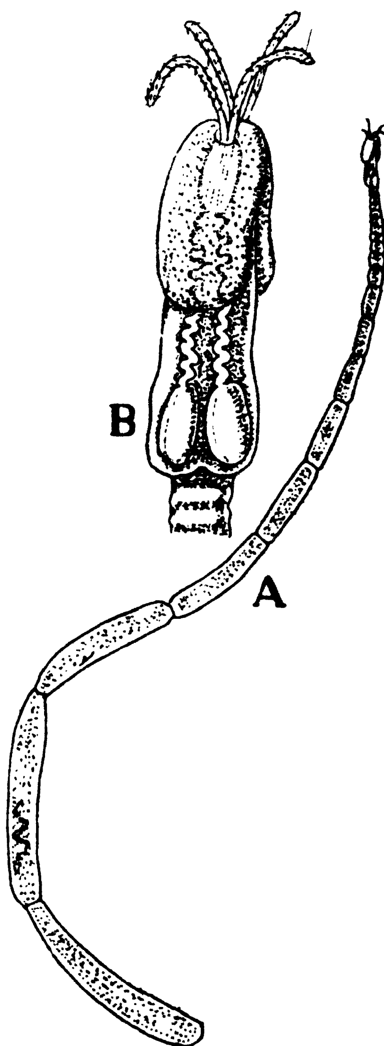


Fig. 36.—*Tentacularia carcharidis*. A, entire worm, ×20; B, head, ×about 43. (After Shipley and Hornell.)

From *Carcharias melanopterus*, Pearl Banks, Ceylon. Shipley and Hornell.

"Found in the intestine of a *Carcharias melanopterus* taken in Dutch Bay on January 5th, 1905. The length usually 9 mm. The anterior end of the body is extremely thin and whip-like; the body, however, thickens posteriorly until the two last proglottides are 0·5 mm. in thickness. These proglottides are very long, 1·5 mm. and 2 mm. respectively.

"The head is minute, and in stained specimens takes little stain. The two lappets are smooth at their edges, not wrinkled, and with no indentation or sign of division into two. The proboscides are very fine, and bear a number of spines, not hooks. These spines are thicker at the base than at their free end; they all point backwards. They are very minute, and seem to be arranged in slightly oblique rings. The proboscis-tubes are very closely coiled, and end in four muscular bulbs which hardly occupy one-fifth of the total head-length. The whole head seems to be dusted through with granules.

"There is no neck. The narrow, band-like proglottides appear immediately behind the head, and they, and even the hinder proglottides, are separated by quite clear transparent divisions. There are only some eighteen or nineteen proglottides, and we were unable to make out the anatomy of these, as it seemed the material was not very well preserved." (*Shipley & Hornell.*)

Pintner (1913) is of opinion that this species belongs to the genus *Otobothrium* Linton, 1890, and further, that it is possibly synonymous with the type-species of that genus, viz. *O. crenacolle* Linton, 1890.

(9) **Tentacularia leucomelana** (Shipley & Hornell, 1906). (Fig. 37.)

Synonyms:—? *Tetrarhynchus longicollis* van Ben., 1850.
Tetrarhynchus leucomelanus Shipley & Hornell, 1906.

From (1) *Dasybatus sephen*, Pearl Banks, Ceylon. Shipley and Hornell. (2) *Rhynchobatus djiddensis* and *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

Shipley and Hornell gave the following account of this species:—"5 cm. to 8 cm. long, with posteriorly thick, stout proglottides, 3 mm. broad. Anterior half or two-thirds of the preserved body white, the remainder slaty black, deepening into a dense black. When alive, milky white, with a pink patch behind the proboscis sheath. Head with shallow lappets well defined. Proboscides with an enormous number of very minute teeth, all of uniform size and shape, arranged in rings and longitudinal rows. The proboscis sacs are very long, occupying seven-tenths of the length of the head. There is a short neck; the posterior edge of each proglottis is salient. Generative pores irregularly alternate."

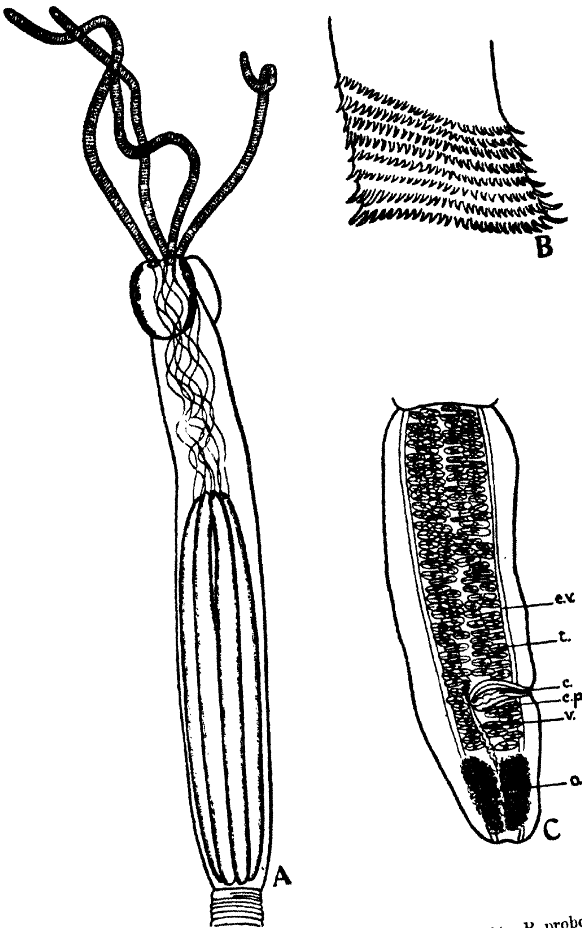


Fig. 37.—*Tentacularia leucomelana*. A, head, × 24; B, proboscis hook × 232; C, mature segment, × 75. (After Southwell.)

In all the specimens except one the strobila had broken off close to the head, so that only a few immature segments were seen. The head is characteristic and can be identified by the following points :—(1) It measures about 7 mm. in length. (2) The proboscis sacs are usually half, but sometimes seven-tenths the length of the head. (3) There are two comparatively small bothridia, measuring only 360 μ in length. (4) The free portions of the proboscides are very long indeed, and are armed with innumerable minute, delicate, slightly curved, sickle-shaped hooks all alike, but varying in length from about 8 to 15 μ and arranged spirally. Segmentation begins immediately behind the head ; the genital pores are irregularly alternate, and are situated in the posterior third of the segment. The worm is composed of about forty segments, the last one measuring 1·8 mm. in length and 400 μ in breadth.

Testes and Vas deferens. The testes are numerous and confined to the central field ; they extend on both sides to the ovary and are of an oval shape, with their axes at right angles to the length of the segment. The cirrus pouch is large and extends over half the breadth of the segment. As usual, the cirrus lies coiled within the pouch : it was not determined whether it was armed.

Ovary and Vagina. The ovary is U-shaped, composed of a number of lobes, and is situated at the extreme posterior extremity. The course of the vagina could not be followed as only one strobila was mature and could not be sectioned, but in one segment it opened ventrally and slightly posteriorly to the cirrus pouch.

Vitelline Glands. The vitelline glands encircle the segment, and in whole mounts obscure the anatomy.

Uterus. The uterus was rudimentary and consisted of a central stem. No eggs were seen.

This species is very closely related to, if not identical with, *Tetrarhynchus longicollis* van Ben., 1850.

(10) Tentacularia binunca (Linton, 1909). (Fig. 38.)

Synonym :—*Rhynchobothrium binuncum* Linton, 1909.

From *Dasybatus* sp. (*walga* ?), Pearl Banks, Ceylon. Southwell.

The species is distinguished by the peculiarly shaped hooks on the proboscides, by the worm being composed of about seven segments,—the last being almost as large as the remainder of the worm,—and by the pore being situated in the posterior third of the segment.

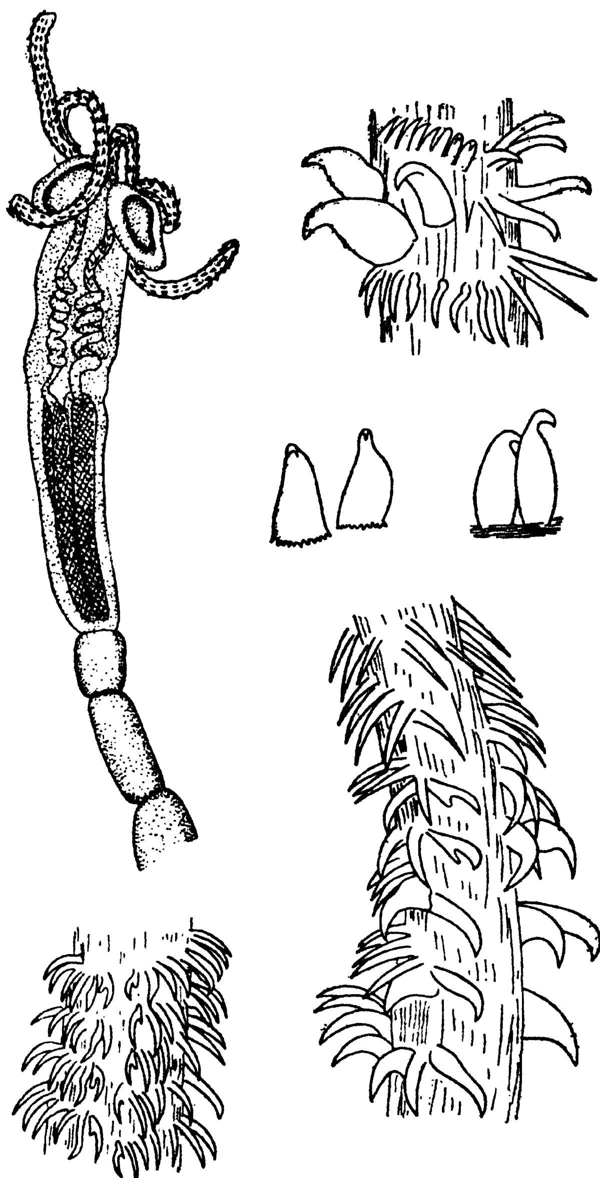


Fig. 38.—*Tentacularia binunca.* Head and proboscis hooks, magnification unknown. (After Linton.)

(11) **Tentacularia spinulifera** (Southwell, 1911). (Figs. 39 & 40.)

Synonyms :—*Tetrarhynchus spinuliferus* Southwell, 1911.
Rhynchobothrium laciniatum Yoshida, 1917.

From *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Southwell.

The worm measures up to 5·5 cm. in length, and the greatest breadth is 1 mm. It is composed of a large number of seg-

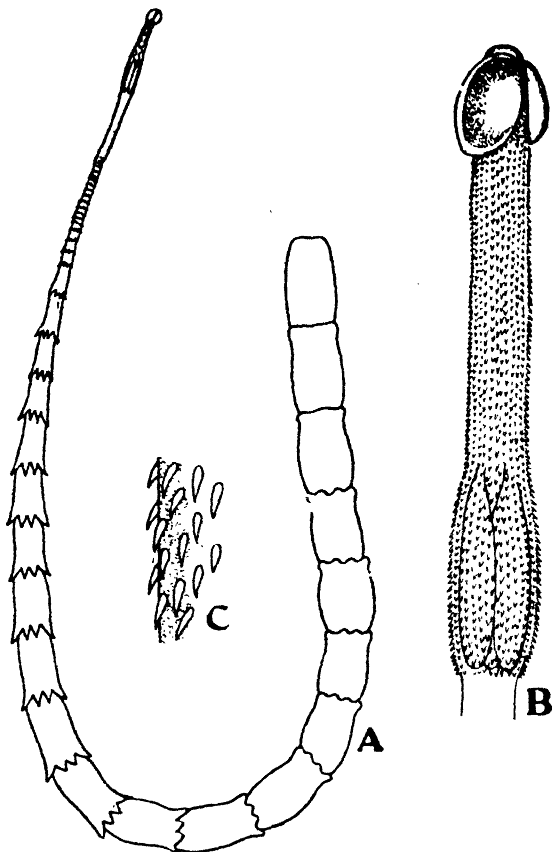


Fig. 39.—*Tentacularia spinulifera*. A, entire worm, × 6 ; B, head, × 50 ; C, proboscis hooks, magnification unknown. (After Southwell.)

ments, the last measuring about 1·3 mm. in length. The posterior margins of the segments are produced into long digitate flaps with pointed extremities ; these laciniæ are small in the neck region and short and blunt in gravid segments.

The pores are situated laterally at the junction of the anterior two-thirds and posterior third of the segment. Uterine pores are present on the ventral surface ; the segments do not leave the chain until the uterus is fully mature. The neck is short, measuring only about 250 μ.

Head. The head is very small, measuring 1 mm. in length ; its breadth at the bulbs is 120 and in the vicinity of the sheaths 76 μ ; the two bothridia measure 126 in length and 90 μ in breadth ; the proboscis sheaths form long, dense, spiral coils, and the proboscis sacs measure 280 in length and 27 μ in breadth. Unfortunately the proboscides were not protruded, and consequently details relating to the spines cannot be given. The entire head is covered with very minute spines.

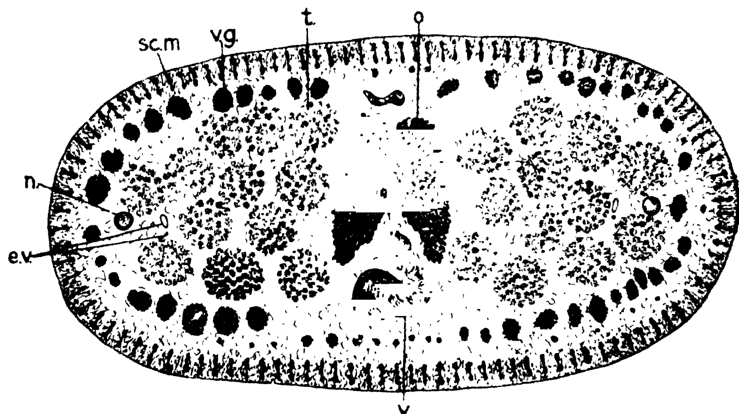


Fig. 40. *Tentacularia spinulifera.* Transverse section of mature segment, × 185. (After Southwell.)

Muscular System. The parenchyma is not divided into cortical and medullary parts. The longitudinal muscles consist of a number of small bundles in a single layer situated immediately beneath the cuticle. Transverse and dorso-ventral fibres were not seen.

Excretory System. The excretory vessels are both very small, but the ventral one is larger than the dorsal and is situated immediately beneath it.

Nervous System. A rather large longitudinal nerve runs along each margin of the strobila laterally to the excretory vessels.

Testes. The number of testes could not be counted, as the worms were not well preserved.

Vas deferens. The cirrus pouch is large, extending to the median longitudinal axis of the segment. The cirrus is dilated

near the pore, and a number of coils of the vas deferens lie within the pouch. Outside the pouch the vas deferens forms a small coiled mass near the median extremity of the pouch.

Ovary. This is a bilobed organ situated posteriorly and composed of a few, large, club-shaped acini. When fully mature, the acini appear to fuse on each side, giving the ovary a dumb-bell appearance.

Vagina. Unfortunately details relating to this organ could not be made out.

Vitelline Glands. These encircle the entire segment and are composed of large acini.

Uterus. This develops early as a tube with very thick lobulated lateral walls; it eventually fills the entire segment. A uterine pore is situated ventrally near the median extremity of the cirrus pouch; it has a muscular margin.

Eggs. No fully ripe eggs were seen; of those observed some were flask-like, with a number of short filaments at one end, whilst others were somewhat kidney-shaped, with a number of short filaments at both extremities.

There is no room for doubt that *R. laciniatum* Yoshida 1917, is identical with *T. spinulifera* Southwell, 1911.

(12) **Tentacularia rossi** (Southwell, 1912). (Fig. 41.)

Synonym:—*Rhynchobothrium rossi* Southwell, 1912.

From *Dasybatus kuhli*, *D. walga*, *Rhynchobatus djiddensis*, and *Stoasodon narinari*, Pearl Banks, Ceylon. Southwell.

The writer, in his original work on this parasite, was unable to give its anatomical details. A full description is now available.

The worms measure up to 6 cm. in length, and the maximum breadth is about 2 mm. There is a large number of segments, which normally have slightly salient margins, but when the worm is contracted this characteristic is much more pronounced in the anterior part of the worm. The largest posterior segment measured 4 by 2 mm. The genital pores are irregularly alternate and situated a little posteriorly to the centre of the lateral margin of the segment. The worm is very thin and whip-like anteriorly, broadening out rapidly posteriorly. The neck is short, measuring about 600 μ.

Head. The head varies in length from 2 to 3·2 mm. It has a fairly even breadth of 450 μ both across the proboscis sacs and anteriorly. The posterior part of the head merges insensibly into the strobila, the junction between the two being marked by the fact that the tissue of the strobila is denser than that of the head. The proboscis sacs are situated midway between the anterior and posterior extremities of the head; they measure 700 μ in length and 100 μ in breadth.

The proboscides are comparatively very short. Within the head they pursue a slightly wavy course. Their free portion, anterior to the head, is also very short; they are armed with numerous very minute spines 4 or 5 μ only in length. There are two bothridia, almost circular in outline, and having a length of 500 μ.

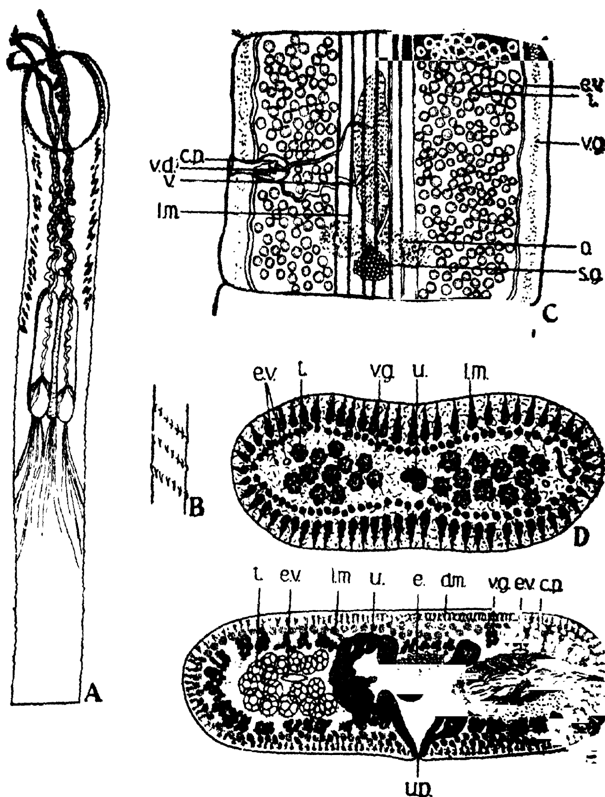


Fig. 41.—*Tentacularia rossi*. A, head, × 30: B, proboscis hooks, × 400; C, mature segment, × 54; D, transverse section of mature segment, × 40; E, transverse section of nearly gravid segment, × 46. (After Southwell.)

Excretory System. The ventral excretory vessel on each side is large and prominent. The dorsal one is extremely small, and can rarely be seen even in sections. The cirrus pouch lies ventral to the dorsal vessel.

Nervous System. On each side there is a nerve running the length of the worm and situated externally to the ventral excretory vessel.

Muscular System. The cuticle has a thickness of 12 μ. Immediately beneath it is a rather large outer layer of dorso-ventral muscles. Internally to the latter is a single layer of very large longitudinal fibres, median to which lie a few delicate circular ones. Oblique fibres can be seen ramifying between the longitudinal bundles. The vitelline glands lie internally to the longitudinal muscles.

Testes and Vas deferens. The testes are numerous and are situated laterally, *i. e.*, they are absent from the central field. On the pore side a number of testes occur posteriorly to the cirrus pouch. The cirrus pouch is small, 180 by 145 μ, and occupies one-seventh the breadth of the segment. It lies internally to the ventral excretory vessel and opens at the base of a deep pit or genital sinus. The cirrus is coiled within the pouch and is unarmed. Outside the pouch the vas deferens is very short.

Ovary and Vagina. The ovary is bilobed or U-shaped, with the free extremities posterior; it is situated posteriorly and is granular in appearance. The vagina, just anteriorly to the ovary, dilates into a receptaculum seminis, and, pursuing a very coiled course, opens into the genital sinus, ventrally to the cirrus pouch. Posteriorly to the ovary there is a large and conspicuous shell gland.

Vitelline Glands. These are confined to the lateral margins; in cross section they present a semicircular distribution. The glands are entirely absent from the mid-dorsal and mid-ventral areas; further they lie internally to the longitudinal muscles.

Uterus. As usual, this arises as a central longitudinal stem. As it becomes gravid, large lateral branches arise on each side. Eventually it fills the segment entirely and opens to the exterior ventrally in the middle of the segment by a definite primary pore.

Eggs. The uterus was full of eggs tightly packed together, making measurement difficult; they were about 45 μ in length and 22 μ in breadth, and at one pole they bear two or three filaments measuring 8 to 10 μ.

(13) **Tentacularia ilisha** (Southwell & Prashad, 1918). (Fig. 42.)

Synonym :—*Rhynchobothrius ilisha* Southwell & Prashad, 1918.

From *Carcharias gangeticus*, Bengal, India. Southwell and Prashad. Larval forms from *Clupea ilisha*, same locality and collectors.

Bothria two, lateral, entire, rounded, external face hollowed to form a sucking disc, widely separated posteriorly and approximated anteriorly. Neck shorter than the head, flat. Proboscides filiform and armed with four kinds of hooks

arranged in oblique circles, the larger ones being distributed principally on the outer surface. Anterior segments shallow and numerous. Last one much longer than broad. Total number of segments about 232. Genital apertures

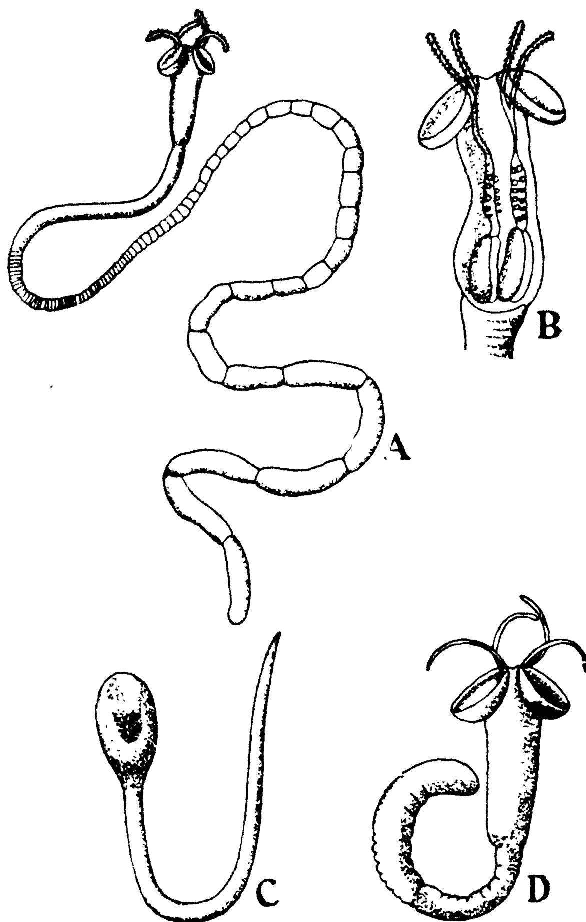


Fig. 42.—*Tentacularia ilisha.* A, entire worm; B, head; C, cyst from muscle of hilsa; D, young worm from stomach of shark. Magnification unknown. (After Southwell and Prashad.)

irregularly alternate and situated about the posterior third of the proglottid. Length of worm 11·5 cm. Posterior segments separating in twos and threes.

The head is large compared with the size of the worm, and measures 4·2 mm. in length. The breadth of the anterior

extremity is 2·6 mm. and of the posterior extremity 1·4 mm. Length of bothridia 1·8 mm.; of proboscides 2·1 mm.; of proboscis sacs 1·6 mm.

The bothridia are paired, approximated anteriorly and widely separated posteriorly. They are round in shape, having entire margins and sucker-like external surfaces. The proboscides are four in number; the armed portion is very short, with an equal length unarmed and very long tubes connecting them to the proboscis sacs. The hooks are of four types arranged in oblique rings, the larger ones being disposed along the outer margins. As usual, the hooks towards the base of the proboscides are much smaller than the rest.

The neck is short, measuring only 2·2 mm. It is flattened and not cylindrical. The anterior proglottides are shallow and numerous. The posterior ones are much longer than broad, measuring 5·1 by 1·3 mm. The male genital organs appear first. The female organs are to be seen only in the last few proglottides. Of the male organs, the testes are first visible about the middle of the worm. The genital aperture is situated at about the posterior third of the proglottis, and the male aperture is immediately in front of that of the female.

Nervous System. This consists of a single fine nerve on each side, external to the water-vascular system.

Excretory System. This consists of a single pair of broad tubes, situated one on each side. They communicate with each other by a wide transverse vessel situated at the posterior margin of each segment. In the head they break up into a series of fine vessels.

Testes. These are numerous, occupying the greater part of the mature proglottid; they first appear laterally. From each is given off a minute tubule; these unite later to form the vas deferens. This is a thick coiled tube originating a little in front of the ovary and opening directly into the cirrus sac. The vesicula seminalis is a bag-like structure situated close to the junction of the vas deferens and the cirrus sac. The cirrus is fairly long and lies coiled up in the spacious cirrus sac; it is apparently unarmed.

Ovary and Oviduct. The ovary is bilobed. From each lobe a very small oviduct arises. The two oviducts unite in the middle line and receive, at the point of junction, the duct of the shell gland. This organ lies between the lobes of the ovary in the centre line. The uterus originates anteriorly from the point of union of the two oviducts; it runs forward in the middle line as a blind diverticulum, practically to the anterior termination of the proglottid, narrowing as it goes. The vagina also originates close to the mouth of the uterus, and is continued as a narrow coiled tube to near its

opening. It then widens to form a barrel-shaped receptaculum seminis.

Life-history. A partly digested hilsa was found in the stomach of a shark by Southwell and Prashad, and all stages in the development of this worm were observed by them. The cysts were tadpole-shaped, and consisted of a club-like head and a long tail-like structure which was capable of considerable movement and appeared to serve the purpose of mooring the larva in the intestine of the shark during the digestive processes.

The head in one specimen measured 4·8 by 3·6 mm. The tail tapered to a point and measured 5·2 cm. in length. On opening out the "head," the larva was seen to be a massive structure occupying the greater part of the head and lying in a coiled position. The tips of the four proboscides were just everted and the spines could be clearly seen. Many young worms were also obtained from the lumen of the intestine. These had not had time to attach themselves to the intestine of the host.

(14) **Tentacularia johnstonei** Southwell, 1929. (Fig. 43.)

From *Dasybatus sephen*, Pearl Banks, Ceylon. Hornell.

The worms are relatively large and stout, measuring up to 5 cm. in length and having a maximum breadth of 1·5 mm. They are composed of numerous, rather thick segments, with slightly salient posterior margins, the last segment measuring 2 mm. in length and 1·4 mm. in breadth; the genital pores are irregularly alternate and are situated in the posterior third of the segment.

Head. The head is very small and somewhat heart-shaped, the pointed extremity being directed anteriorly. It has a maximum breadth of 900 and a length of 900 μ. The two bothridia are small, having a breadth of 530 and a length of 500 μ; their margins are entire and only slightly thickened. The proboscis sacs are situated almost immediately behind the posterior margins of the bothridia, and they have a length of 245 μ and a maximum breadth of 110 μ. The neck measures about 220 μ in length; anteriorly it is somewhat thickened and the posterior extremities of the proboscis sacs lie in the thickened portion. The armed portions of the proboscides and the proboscis sacs are each about as long as the bothridia.

Hooks. The hooks on the proboscides are arranged in spirals. The internal dorsal face of each proboscis bears two longitudinal rows of rose-thorn-shaped hooks, 10 μ in length, arising from a base also 10 μ in diameter. Ventrally there are three or four longitudinal rows of smaller rose-thorn-

shaped hooks, one or two longitudinal rows of which have their points directed anteriorly.

Muscular System. The longitudinal muscular system is strongly developed and consists dorsally and ventrally of a single row of oval bundles. Laterally these are much smaller and scattered about irregularly.

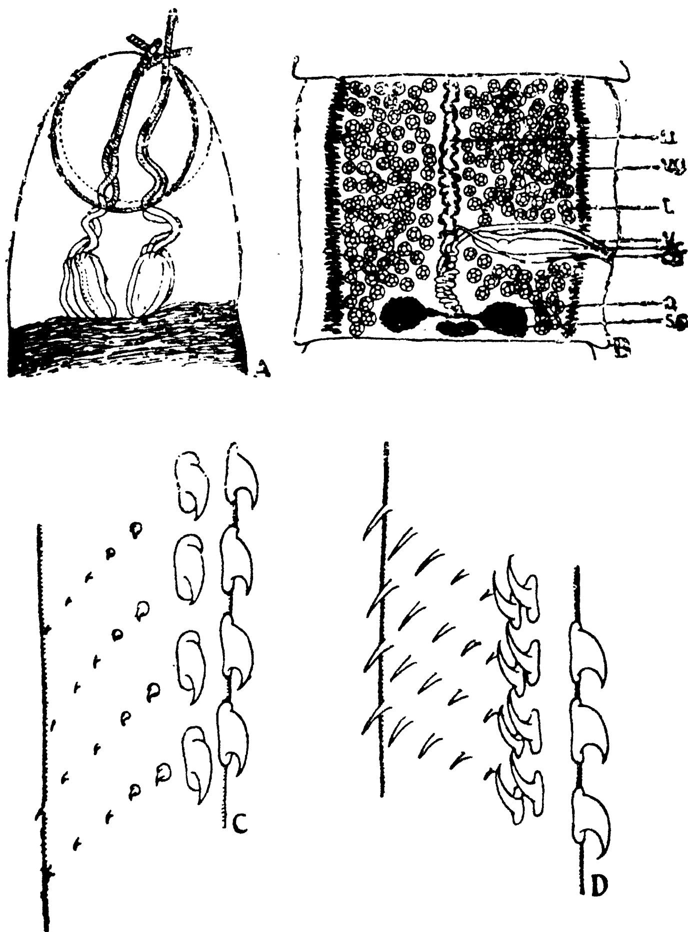


Fig. 43.—*Tentacularia johnstonei.* A, head, × 46 ; B, mature segment, × 46 ; C, D, proboscis hooks, × 660. (After Southwell.)

Excretory System. A large internal and a small external vessel run along each lateral margin of the segment.

Details of the nervous system were not investigated. The cortical and medullary parenchyma are strongly developed.

Testes and Vas deferens. The testes are very numerous, and fill the dorsal part of the segment in front of the ovary. In the early stages of development they are crowded together in the median field on each side of the antero-posterior axis. The cirrus pouch is conspicuous, and extends one-third the distance across the segment; no spines were observed on the cirrus. Posteriorly and median to the pouch the vas deferens forms a number of conspicuous coils.

Ovary. This is, as usual, a bilobed organ situated posteriorly; the vagina is a short coiled tube which runs ventrally (?) to the pouch and opens to a shallow genital atrium.

Vitelline Glands. These completely encircle the segment and are situated in the cortical parenchyma.

Shell Gland. This is a conspicuous organ lying posteriorly to the ovary.

Uterus. This arises as a closely coiled tube running to the extreme anterior margin of the segment; eventually it entirely fills the segment and is distended with eggs, none of which, however, were mature in the observed specimens.

In a former paper the writer considered this species as identical with *T. rhynchobatidis* Shipley & Hornell, 1906, and also with *R. curtum* Linton, 1909. A re-examination of the old and of fresh material has proved that the species is quite distinct, and also that *R. curtum* Linton, 1909, is distinct from *T. rhynchobatidis* Shipley & Hornell, 1906. *T. johnstonei* Southwell, 1929, is differentiated from all other tetrarhynchids except *T. obesa* by the form of the head and the arrangement of the hooks on the proboscides.

(15) **Tentacularia michiæ** Southwell, 1929. (Fig. 44.)

From (1) *Rhynchobatus djiddensis* and *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell. (2) *D. sephen*, Pearl Banks, Ceylon. Pearson.

The worms measure 1·8 cm. in length and the maximum breadth is 800 μ. They are composed of about twenty segments. The thirteenth or fourteenth segment is square, measuring 270 μ: the last segment is full of eggs and measures 3 mm. in length and 800 μ in breadth. There is no neck. The genital pores are irregularly alternate and are situated in the posterior third of the worm; the pores frequently show tumid lips.

Head. The head measures 4·2 mm. in length; the proboscis sacs are 2·6 mm. in length and 216 μ in breadth.

There are two small, somewhat circular bothridia having a length of 450 μ. The anterior and lateral portions of the head are armed with minute deciduous spines measuring about 6 μ. The proboscides are extremely long, certainly longer

than the entire head, and the free portion extending beyond the head is also very long. They are very densely armed

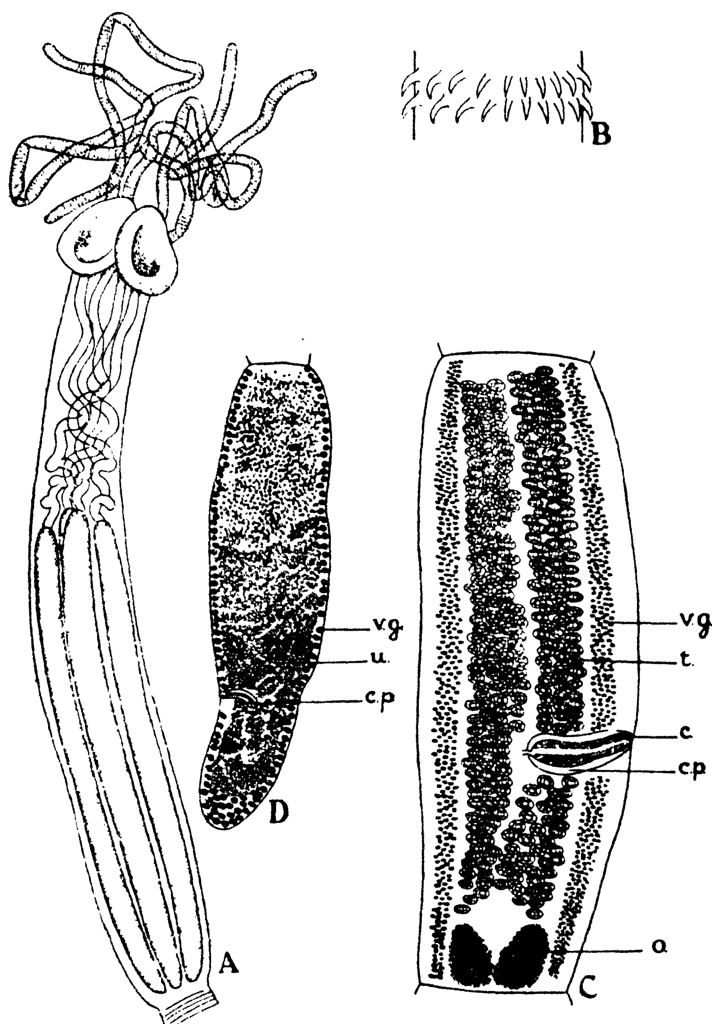


Fig. 44.—*Tentacularia michiæ.* **A**, head, × 26; B, proboscis hooks, × 500; C, mature segment, × 75; D, gravid segment, × 23. (After Southwell.)

with extremely delicate minute hooks, all alike, which measure about 13 μ, giving the proboscis the appearance of being covered with fine fur.

The genital organs call for no comment; in the last segment they have all disappeared except the cirrus pouch.

The vitelline glands encircle the segment at the posterior extremity only.

(16) **Tentacularia obesa** Southwell, 1929. (Fig. 45.)

From *Dasybatus sephen*, Pearl Banks, Ceylon. Southwell.

The worm measures 1·1 cm. in length and has a maximum breadth of 1 mm. For its length it is very stout and fleshy. It is composed of about 30 segments, of which roughly 20 immediately behind the head are very small, and can only be counted under low-power magnification.

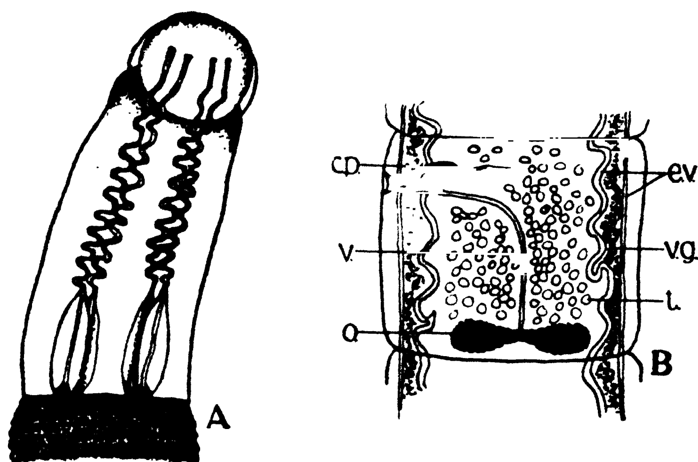


Fig. 45.—*Tentacularia obesa*. A, head, × 30; B, mature segment, × 33. (After Southwell.)

The genital pores are irregularly alternate and are situated laterally in the anterior sixth of the segment. The last gravid segment is about 1 mm. square.

Head. The head measures 2 mm. in length and 800 μ in breadth. It is extremely conspicuous because it is semi-transparent, while the rest of the worm is densely opaque, the junction between the two being very pronounced. There are two simple bothridia measuring 500 μ in length and 550 μ in breadth. The proboscis sacs are situated in the posterior quarter of the head close to the first segment. They measure 540 μ in length and 160 μ in breadth. The proboscides were not protruded, and hence it is impossible to describe the hooks; but they appeared to be all alike, simple, slender, recurved, and to measure about 12 μ.

Testes and Vas deferens. As only one worm was obtained, it is impossible to describe the genital organs in detail. The testes are well developed in the tenth segment, and in the twentieth they fill the centre of the proglottis, extending backwards as far as the ovary on both sides.

The cirrus pouch is a cylindrical organ situated in the anterior sixth of the segment and extending in the median direction about one-fifth the breadth of the proglottis. No details relating to the cirrus or vas deferens could be made out.

Ovary. This is small, situated posteriorly, and from it the vagina runs to the pore, in a broad curve, as a very wide conspicuous duct.

Vitelline Glands. These appear to be limited to the lateral margins. There is a large shell gland posteriorly to the ovary.

Uterus. This is a wide sac entirely filling the segment. The shape and the size of the eggs could not be determined.

This species is characterized by the transparent head and by the short obese strobila. The head bears a general resemblance to that of *T. johnstonei* Southwell, 1929; it differs from it, however, in size and in the position of the genital pore.

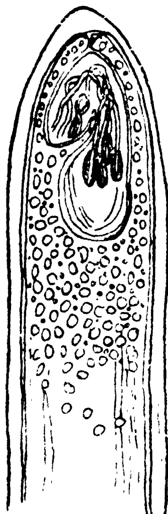


Fig. 46.—*Tentacularia pinnæ*. Cyst, magnification unknown. (After Shipley and Hornell.)

(*b*) Larval Forms.

(17) **Tentacularia pinnæ** (Shipley & Hornell, 1904). (Fig. 46.)

Synonym :—*Tetrarhynchus pinnæ* Shipley & Hornell 1904.

From *Balistes stellatus*, *B. mitis*, and probably *Pinna* sp., Pearl Banks, Ceylon. Hornell.

"The advanced larva, or metacestoid, is enclosed in a large vesicle, which not only covers the head, but the entire body, and is much larger than the body, 1 mm. to 15 mm. long. The teeth on the introvert are very numerous and arranged in oblique lines. Each tooth is slender, very slightly hooked, and is shaped like a Malay kriss. The proboscis sheaths extend nearly to the posterior end of the scolex. Two lappets." (*Shipley & Hornell.*)

(18) **Tentacularia spiracornuta** (Linton, 1907). (Fig. 47.)

Synonym:—*Rhynchobothrius spiracornutus* Linton, 1907.

Larvæ only, from *Caranx* sp. and *Thynnus* sp., Pearl Banks, Ceylon. Pearson.

The total length of the larva, or head, with its attached blastocyst is 9 mm.; the blastocyst measures 3 mm. in length and the larva (head) 6 mm. The blastocyst has a breadth of 500 to 600 μ. The breadth of the head across the bothridia is 600 μ, across the proboscis sacs 470 μ, and across the portion between the sacs and the bothridia the breadth is 300 μ. There are two simple bothridia having a length of 630 μ. The proboscis sacs are 900 μ, *i. e.*, they are between one-sixth and one-seventh the total length of the head. The hooks on the proboscides are very densely crowded together. On one face of the proboscis the hooks are for the most part long and thin, and vary in length from 30 to 38 μ. Along one margin of the same surface, however, they are more thorn-shaped, stout, and have a length of 30 μ. On the other surface of the proboscis there are a number of simple curved hooks similar to those on the opposite surface of the proboscis, but measuring only about 20 μ. Marginally these grade into numbers of very small hooks which measure 10 μ only.

The specimens agree closely with Linton's description of this species. He obtained the larva from cysts on the viscera of *Epinephalus maculosus* and *Paranthias furcifer*. The length of the head to the base of the bulbs was 5 mm. The length of many of the hooks was 24 μ. He described the worm as follows:—"Head usually broader than long, orbicular or cordate; bothria lateral—that is, coinciding with the lateral margins of the body—with raised borders; neck long, slender, nearly linear, enlarging at base, sometimes appearing to begin abruptly by an articulation with the head, and usually abruptly larger than the anterior end of the body; proboscides much shorter than neck, with a tendency to coil up into rather close spirals when everted; sheaths nearly straight, bulbs long-ovate, retractor muscle attached to posterior end. The hooks

are of many different shapes and sizes, but on account of the similarity of the hooks which make up the several longitudinal

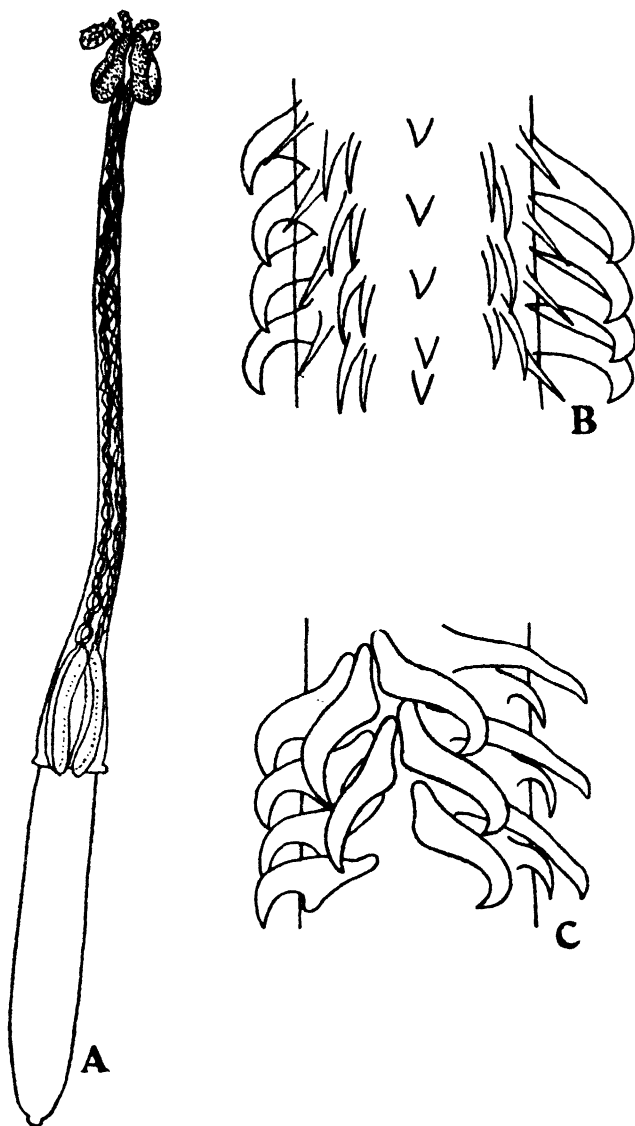


Fig. 47.—*Tentacularia spiracornuta.* A, larva, × 18; B, C, proboscis hooks, × 500. (After Southwell.)

rows, the general effect is that of uniformity and symmetry. There is some resemblance in the arrangement of the hooks

to that of *R. speciosum*, particularly in the case of one of the longitudinal rows, where the small hooks of which it is composed are placed by twos on account of the lengthening of alternate intervals between the hooks of the row. A characteristic feature of this species is the distinctness of the longitudinal rows of hooks. There was no indication of segments."

The larva also resembles the head of *T. benedeni* Vaull., 1899, but is very much larger.

(19) **Tentacularia macfiei** Southwell, 1929. (Fig. 48.)

Synonyms:—*Rhynchobothrius* spp. I., III., A, B, & C, Southwell, 1912.

Encysted larval forms only from (1) *Chorinemus lysan*, *C. toloo*, *Lutjanus argentimaculatus*, *L. gibbus*, *Serranus undulosus*, *Balistes mitis*, *B. stellatus*, *Balistes* sp., *Psettodes erumei*, Pearl Banks, Ceylon. Southwell. (2) *Cybium guttatum*, Pearl Banks, Ceylon, and *C. guttatum*, *Cossyphus axillaris*, and *Trichiurus savala*, Ceylon. Pearson.

It is very probable that one of the larvæ figured by Shipley and Hornell, 1906, from *Balistes mitis* (viz., pl. ii, fig. 27) is the same species.

Southwell described the cysts and larvæ in 1912, stating that the former measure about 1·2 cm. by 4 mm. and are milky white in appearance. The larvæ were about 7 mm. by 600 μ. The head bears two bothridia, each one emarginated posteriorly. The hooks were stated to be all alike, but such is not the case. It is practically certain that the five larvæ described as *Rhynchobothrius* spp. I., III., A, B, & C, and figured by Southwell (1912, p. 272, pl. iii, figs. 31, 32, 33, 34, and 35) from *Serranus undulosus*, *Lutjanus gibbus*, *Psettodes erumei*, and *Balistes mitis* respectively, are identical with those from *Cybium guttatum*. Additional material from the latter host has been obtained and examined, and the writer is now able to add the following details.

The cysts and the larvæ vary considerably in size in different species of fishes and even in one host; they merely represent growth stages.

The cysts are semi-transparent, milky white, club-shaped, or oval with broad ends, measuring about 7 by 4 mm. The larva is attached by the extremity of its head to one end of the cyst, and measures up to 5 mm. in length. The breadth across the proboscis sacs is about 800 μ; across the bothridia it varies, and across the rest of the head is about 700 μ. There are two bothridia, each emarginated posteriorly. They have a length of about 900 μ and a breadth of about 800 μ. A cluster of cilia runs parallel

to the margin of each bothridium arising on each side of the posterior indentation and gradually disappearing anteriorly. The proboscis sacs have a length of 1·1 mm., *i. e.*, they are approximately one-quarter the length of the head.

The four proboscides lie much coiled within the head. They are armed with closely set hooks of different shapes and sizes as shown in fig. 48. Posteriorly the larva carries a blastocyst which varies in length from about 1 to 5 mm.

The appearance and size of the head and the hooks of this worm bear a somewhat close resemblance to an adult figured by Linton in 1909 under the name *Rhynchobothrium* sp. He obtained a single specimen from *Ginglymostoma cirratum*. His description is as follows :—" Bothria foliaceous, but with margins somewhat thickened ; head much broader than neck ; neck slender, cylindrical, enlarging at bulbs ; sheaths in close spirals ; bulbs long-oval, with retractor muscle attached at about the middle of the length on the median wall ; proboscides long, hooks of different sizes and shapes. The most marked differences are to be seen in those hooks which are near the base of the proboscides. On one side there are some small straightish spines ; on the other they are much larger, long and nearly straight, but with an abrupt curve at the apex. A single row of these large hooks extends around to the opposite side a short distance from the base. The proboscides were not seen fully extended. So far as seen, the hooks on one side remain small slender and very sharp-pointed, but grow larger toward the apex, so that in the completely everted proboscis the difference between the hooks of the opposite sides is probably slight. The large hooks with abruptly recurved ends are confined to the basal region. Beyond the base the larger hooks become rather broad in lateral view, and are strongly and uniformly curved. On the other hand, among the small hooks, some distance from the base, are hooks which are straightish with abruptly curved tips. Towards the tip of the proboscis, as may be seen in the retracted part, a prevailing form is a slender hook curved in two directions, like a letter S nearly straightened out.

" Transverse striæ begin immediately below the neck. The first distinct segments are shorter than broad, but soon become as long as broad. They then rapidly and uniformly lengthen, but remain about the same breadth. The posterior segments are nearly ten times as long as broad, and their anterior ends are abruptly larger than the posterior end of the preceding segment. None of the segments were mature, although rudiments of reproductive organs could be made out. In the next to the last segment the rudiment of the cirrus bulb was a little behind the posterior third, and the ovary was at the posterior fifth. The anatomy of the posterior

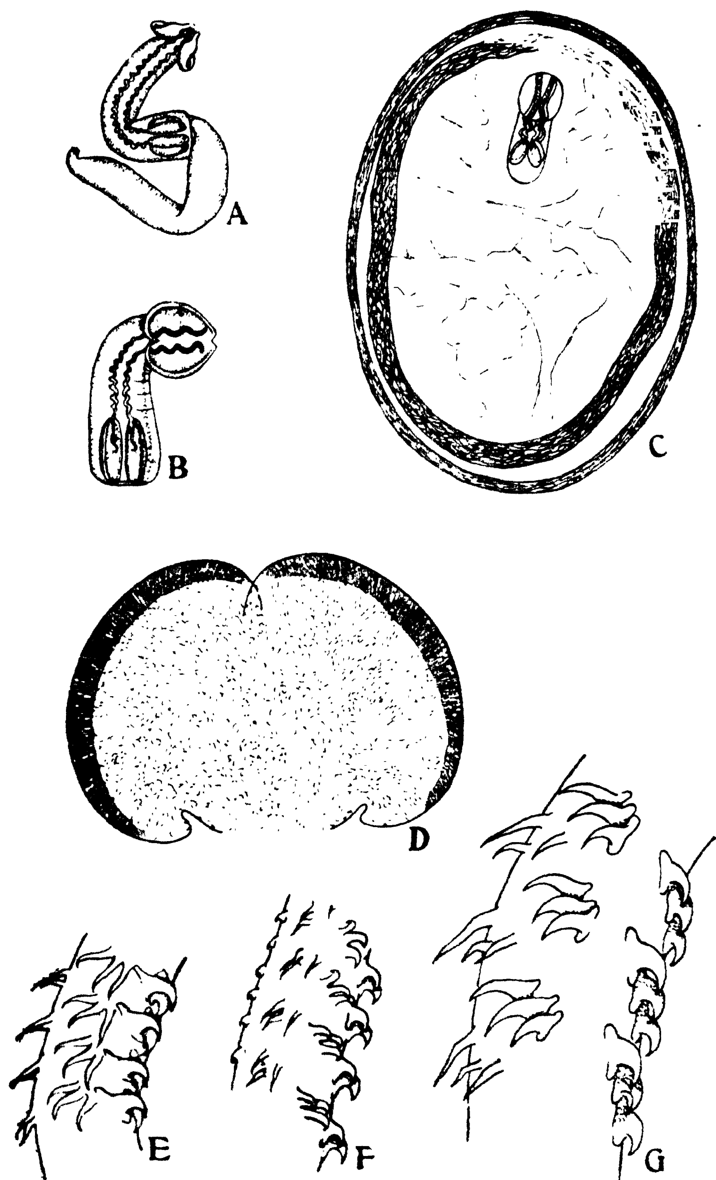


Fig. 48.—*Tentacularia macfiei.* A, larva (= *Rhynchobothrius* sp. I., Southwell, 1912); B, larva (= *Rhynchobothrius* sp. III., Southwell, 1912), magnification unknown; C, cyst, × 42; D, a bothridium, × 75; E, F, proboscis hooks, × 214; G, proboscis hooks, × 500. (After Southwell.)

segments, so far as it could be made out, is much like that of *R. exile*.

"Dimensions, in millimetres, of specimen mounted in balsam: Length 15; length of head and neck 2·4; breadth of head 0·73; bothrium, length 0·48, breadth 0·48; bulbs, length 0·64, breadth 0·16; twentieth and last segment, length 2·08, breadth 0·22; proboscis, length, estimated, 3, breadth, exclusive of hooks, base 0·05, near apex 0·04; length of longest hooks, base 0·035, at apex of everted part, about 0·6 from base, 0·028. From spiral valve of nurse shark, *Ginglymostoma cirratum*. July 6th, one."

Although this larval form is very common in various bony fishes on the Ceylon Pearl Banks, the adult has not apparently been found, and as no adult worm with a head and with similar hooks has yet been described, the author considers it to be new.

Tentacularia sp. (Shipley & Hornell, 1906). (Fig. 49.)

From *Balistes mitis*, Pearl Banks, Ceylon. Hornell.

"A very different form of *Tetrarhynchus* larva was also taken. Here there is no enveloping bladder, but the Tetrarhynchid head is attached and protrudes from a vesicle which shows signs of an excretory pore posteriorly. This larva is evidently one of Vaullegeard's first division, of which *T. lingualis* is the type. The larva differs from the form we described under the name of *Tetrarhynchus balistidis*, inasmuch as there is the large vesicle present. The whole length of the larva and head is just under a millimetre. The teeth, as drawn from living specimens, are shown in pl. ii, fig. 27 *a*. The wall of the vesicle, seen under a high power, seems to contain a large number of globules, possibly calcareous bodies." (*Shipley & Hornell.*)

This is probably *Tentacularia macfiei*, Southwell, 1929.

Southwell (1912) described another larval form from *Balistes mitis* as follows:—"The cysts are long, cylindrical, firm, and opaque. They measure 14 mm. by 2 mm. The larvæ measure 2 mm. by 0·6 mm. The bothridia are circular in outline, concave, with thickened overhanging rims, and are indented anteriorly and posteriorly, and each bothridium is divided into two halves by a shallow ridge running parallel to the body. They measure one-third the length of the head and neck. The proboscis sacs also measure about one-third the length of the head and neck. The proboscides are spirally coiled, and do not protrude to the exterior, the pores being closed. The spines are of various sizes and shapes. Some have narrow bases, and are long and slender, with the extremity

bent at right angles. Others are short with a broad base, and are strongly recurved. The arrangement of the hooks could not be ascertained." This species is almost certainly *T. macfiei* (p. 139).

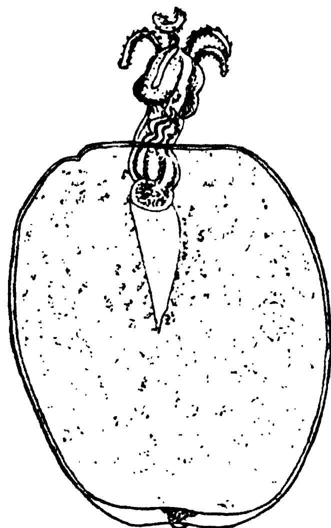


Fig. 49.—*Tetrarhynchus* sp. From *Balistes mitis*, × 75. (After Shipley and Hornell.)

(20) **Tentacularia pillersi** Southwell, 1929. (Fig. 50.)

Larval forms only from (1) *Lutjanus argentimaculatus*, *Drepane punctata*, *Diagramma* sp., *Serranus undulosus*, Pearl Banks, Ceylon. Southwell. (2) Hæmal arch of *Cossyphus axillaris*, Adirampatnam, S. India, and Delft Island, Ceylon, and *Serranus* sp., Negapatam, S. India. Pearson.

In *Cossyphus axillaris* cysts containing larval forms of *Gymnorhynchus gigas* (=*Syndesmobothrium filicolle*) were found amongst the pyloric cæca and also cysts containing *Tentacularia macfiei* Southwell, 1929. Large numbers of adult unencysted trematodes were also found between the pyloric cæca and enormous numbers of immature nematodes, varying in size from 500 μ to 2 cm. Very frequently these nematodes were found adherent to the cysts containing the larvæ of *T. pillersi*, and in practically all such cases the contained cestode larvæ had degenerated. The cysts were oval in shape and measured about 1·2 cm. by 8 mm., although many smaller, and a few larger, were found. They occurred in very large numbers, and often about fifteen would be clustered together like a bunch

of small grapes. In a few of the cysts calcification had commenced and no larva was to be found. Other cysts were full of pus and were likewise sterile. Pus formation also occurred in parts of the surrounding tissue.

The outer cyst has a thin, semi-transparent, but tough wall. It is presumed that this is secreted by the host. The inner wall is very thick and dark brown measuring about 9 by 5 mm. The larva, to which no blastocyst appeared to be attached, is characteristically lancet-shaped, 1·5 cm. in length 3 to 3·5 mm. in breadth posteriorly, and 800 μ to 1 mm. in breadth anteriorly. There are two very small simple bothridia measuring about 700 μ in length and 900 μ in breadth. Their posterior margins are indented. The proboscis sacs are situated posteriorly and measure 4·5 to 5·5 mm. in length and 450 μ in breadth. The proboscides are much coiled throughout the length of the head. About fifteen larvæ were examined. In only one case was a single proboscis everted, and then only to a length of 1·5 mm. Consequently the shape and arrangement of the hooks on the proboscides are not definitely known. The proboscides were dissected out and boiled in caustic soda, and it was found that all the hooks had been dissolved. The opportunity is here taken of noting that when the heads of tetrarhynchids are cleared in pure carbolic acid, the hooks swell and develop "blisters," so that neither their shape nor arrangement can be determined.

The free portion of the protruded proboscis was examined carefully, but only one view was, of course, to be seen; three other proboscides were teased out, so that a number of differently shaped hooks were isolated. They did not appear to be spirally arranged. One surface of each proboscis is covered with small, simple, elongated hooks, varying in size from 65 to 130 μ. On one margin there is a cluster of three curved hooks measuring 90 μ, and at a deeper focus two larger alternating rose-thorn-shaped hooks measuring 130 μ can be seen. Along the other margin there are 3 large rose-thorn-shaped hooks measuring 130 μ, and at a deeper focus two stouter alternating rose-thorn-shaped hooks like those on the opposite margin, also measuring 130 μ, could be seen.

It appears probable that the larva named by Southwell *Rhynchobothrium* sp. II. on p. 271, 'Ceylon Marine Biological Reports' (1912), and figured on pl. xi, figs. 29 and 30, is the same species, although smaller. His description was as follows:—"Large numbers of cysts containing larvæ of a second species of *Rhynchobothrium* were obtained from the mesenteries of various fishes caught during 1908 to 1911. The cysts when preserved are often globular, and measure 15 mm. in diameter. The outer part of the cyst is sometimes gelatinous in nature, and is usually absent. Inside the gelatinous covering is the

cyst proper, which measures 5 by 3 mm., and is either of a milky-white or golden-yellow colour

"The larva itself lies bent in two inside this cyst. It measures 5 mm. long and 1·5 mm. broad posteriorly. The posterior part is 3·5 times the breadth across the bothridia, and the sacs measure almost half the length of the head and neck. The proboscides are coiled, and are not protruded to the exterior, their external openings being closed. The spines are of various sizes and shapes, and do not appear to have any

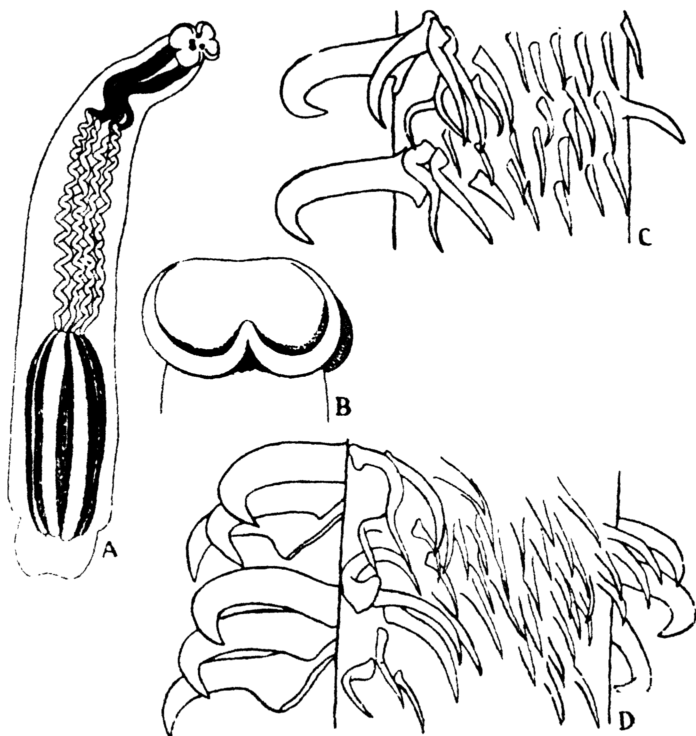


Fig. 50. —*Tentacularia pillersi.* A, larva, × 7 ; B, head, × 35 ; C, proboscis hooks, × 160 ; D, proboscis, × 215. (After Southwell.)

definite arrangement. There are two very small, undivided, saucer-like bothridia having a diameter of barely 0·5 mm. There are no strobilæ."

The species can be easily identified by means of its (1) large size ; (2) lancet shape ; (3) large proboscis sacs and small emarginate bothridia ; (4) hooks. The writer described this larva in 1929, concluding from the above points that it was a new species.

The commoner elasmobranch fishes of Ceylon have frequently been examined for cestode parasites and no worm with a head like that described above has been found; it is therefore probable that the adult worm occurs in one of the large but rarer fishes of this group.

SPECIES INQUIRENDÆ.

(21) **Tentacularia rubromaculata** (Diesing, 1863). (Fig. 51.)

Synonym:—*Tetrarhynchus rubromaculatus* Diesing, 1863.

From *Dasybatus walga*, Pearl Banks, Ceylon. Hornell.

"This is by far the smallest of the tetrarhynchids found in *Trygon walga*. Only two specimens were taken, one measuring 4 mm., the other 7 mm. in length. The head occupies nearly half this length, and the proboscis sheaths, which vary a little in the two specimens, are nearly half the length of the head.

"The bothridia are distinct even when the proboscides are contracted. The latter are four in number and bear sickle-shaped spines, not arranged in very definite rows; between some of them are very short rows of minute, very straight spines.

"Behind the head the body consists of six or seven proglottides; the first two of these are band-like, the third longer, the fourth about square, the fifth twice as long as broad, the sixth and seventh four to five times as long as broad. In one specimen the posterior proglottis bore a lateral eminence, presumably the genital pore, which much resembled the similar process figured by Wagener in a *Tetrarhynchus* taken from a *Trygon pastinaca*.

"In some notes which Mr. Hornell sent with the material he stated that in the bottle which contained the *E. trygonis* were two species of tetrarhynchid, one with collar and the other with red pigment anterior to the muscle sacs. Now, as a matter of fact, there were four species of tetrarhynchids in the bottle, and two of these were collared forms. Thus there is a reasonable degree of probability that the species we are describing, although colourless in spirit specimens, had a reddish patch in front of the muscular proboscis sheaths. In his figure of the *Tetrarhynchus* taken from a *Trygon pastinaca*, Wagener paints a bright red splash just in this place. Neither Wagener's figure nor Diesing's diagnosis, given under the name *Rhynchobothrium rubromaculatum*, descend into any details which might not apply to many tetrarhynchids, yet there is nothing in the figure nor in the diagnosis which differs materially from what we find in our specimens, and on the whole we seem justified in regarding these as belonging to the species *T. rubromaculatus* (Diesing)." (*Shipley & Hornell.*)

Pintner (1913) places this species and *Tetrarhynchus platycephalus* Shipley & Hornell, 1906, in his genus *Lakistorhynchus*, the type-species of which is *Tetrarhynchus benedeni*

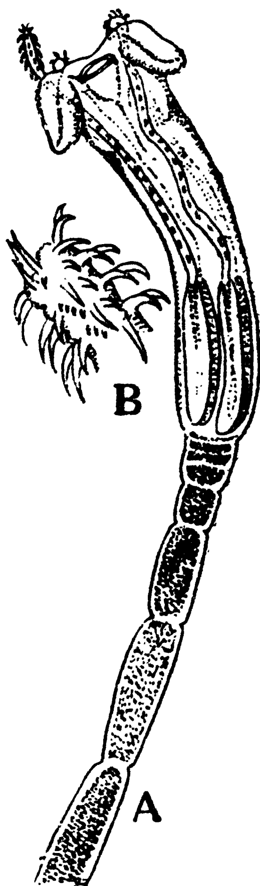


Fig. 51.—*Tentacularia rubromaculata*. A, head and anterior segments, × 40; B, proboscis hooks, magnification unknown. (After Shipley and Hornell.)

(Crety, 1890). He also states that *T. benedeni*=*T. tenuis* van Beneden, 1858=*B. gracilis* Rudolphi, 1819.

It is very doubtful whether *T. rubromaculata* (Diesing, 1863) can be identified from the meagre descriptions and figures given of it, and it is certain that *T. platycephalus* belongs to a totally different group of tetrarhynchids. Shipley

and Hornell figure *T. rubromaculata* with two bothridia. Its identity is quite uncertain.

(22) **Tentacularia unionifactor** (Herdman & Hornell, 1903 *). (Fig. 52.)

Synonym:—*Tetrarhynchus unionifactor* Shipley & Hornell, 1904.

From *Rhinoptera javanica*, Pearl Banks, Ceylon. Hornell.

They are thus described " existing in swarms in the stomach, especially at the pyloric end. Very few were found in the intestine. They occurred in all the specimens of *Rhinoptera javanica* captured. The longest was 3 cm., the other two were about half that length; but Mr. Hornell states that when alive they can extend themselves to 4 or 5 inches. The head and body are stout, averaging a little under a millimetre in diameter; the proboscides are very small and fine, and are invisible to the naked eye. They arise apically, close together at the anterior surface of the head, and are supported by two shallow cephalic suckers or bothridia on each side, which meet anteriorly. The neck extends for 1·5 mm. to 2 mm., and contains the four clearly marked proboscis sheaths and four tubules proceeding from them enclosing the retractor muscles of the proboscides; these are very convoluted. The proglottides are at first broad and shallow, but they soon lengthen, and in the middle of the body they are cylindrical, three times as long as broad, and circular in transverse section; their posterior border just overlaps the succeeding segments, but only just. Posteriorly the proglottides lose their shape, become baggy, and develop a purplish-brown colour, and here they are 2 mm. in length and rather over 1 mm. in breadth.

" The genital openings are irregularly alternate, there being perhaps two pores on the right side, succeeded by two on the left, then one on the right, and so on.

" The anterior proglottides are very shallow, and lie one upon another like a series of saucers or a pile of developing ephyræ: when they deepen a little they have one, rarely two, transverse creases in their cuticle, but as they get to be as deep as they are broad, the number of these creases has very much increased, and the posterior end of the body is quite crinkled.

" The proboscides are armed with hooks which are spirally arranged; the hooks are not very hooked, and the angle is slight; further, all the hooks are shaped alike and are all about the same size. They are very small.

" The two bothridia are comparatively shallow, but during life their edges are obviously very mobile, and they may

* 'Nature,' 10. xii. 1903.

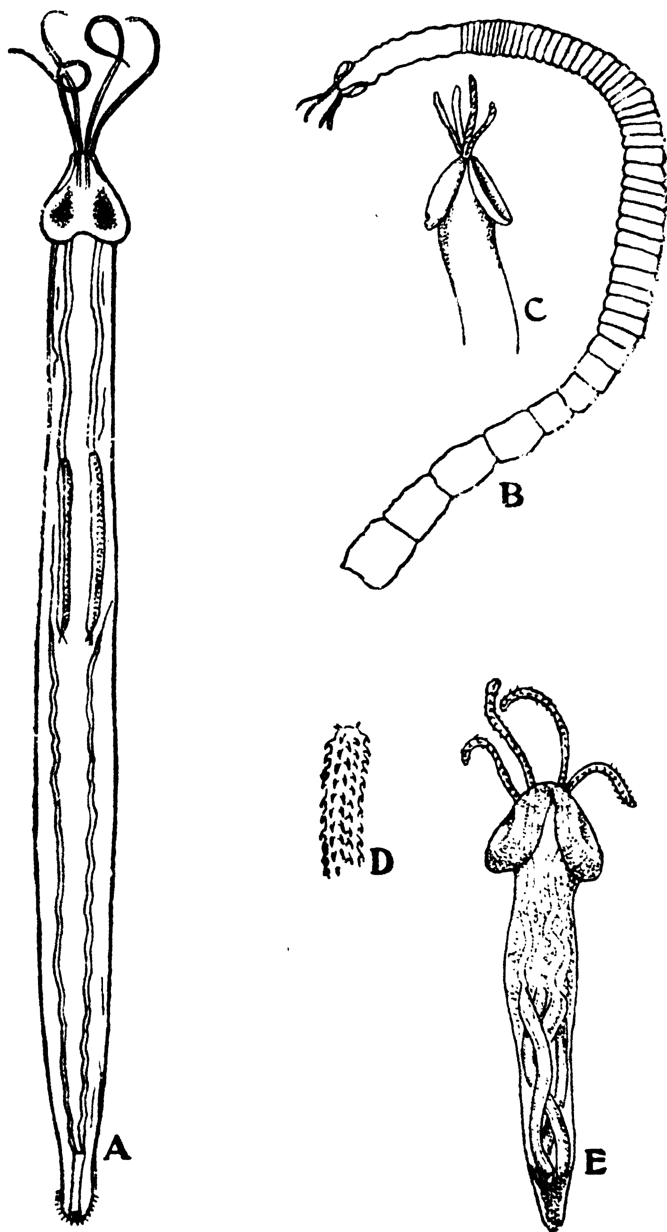


Fig. 52. *Tentacularia unionifactor.* A, larva, magnification unknown; B, entire worm; C, head; D, proboscis hooks, magnification unknown; E, larva, × about 100. (After Shipley and Hornell.)

deepen or become shallower as occasion arises. Their outline is roughly triangular, one angle being anterior. The angles are very rounded, and the deepest part of the bothridium lies in the posterior angles." (*Shipley & Hornell.*)

It is not possible to identify the parasite from the above description. The small hooks, all of the same size and shape, suggest that the worm may belong to the "*lingualis*" group.

It is almost certain that the larval forms named *T. unionifactor* Shipley & Hornell, 1904, from *Margaritifera vulgaris*, belong to the genus *Tylocephalum* Linton, 1890.

Genus III. GYMNORHYNCHUS Rudolphi, 1819.

Synonyms:—*Anthocephalus* Bremser, 1824, and Wagener, 1854.
Pterobothrium Diesing, 1850.
Synbothrium Diesing, 1850.
Acanthorhynchus Diesing, 1850.
Syndesmobothrium Diesing, 1855.

Bosc (1797) erected the genus *Tentacularia* to accommodate a larval tetrarhynchid which he obtained from the liver of *Coryphæna hippurus*.

Cuvier (1817) established the genus *Floriceps* to include certain encysted larval forms of the same group; he also gave the name *Scolex gigas* to a species obtained from *Sparus raji*.

Rudolphi (1819) gave the generic name *Gymnorhynchus* to similar larvæ in which the "body is continuously flattened and tapering, *very long, with a subglobular vesicle in the neck*. With two bipartite bothridia. Proboscides four, retractile, nude." He placed *G. reptans* Rudolphi, 1819, in this genus, giving *Scolex gigas* Cuvier, 1817, as a synonym of *G. reptans*. It has since been shown repeatedly that the proboscides are not nude. It is also true that there is not always a vesicle in the neck.

Bremser (1824), as pointed out by Creplin, Dujardin, and Vaullegeard, gave a figure of Rudolphi's *G. reptans* showing the characteristic vesicle, but he also, on another plate, gave another figure of Rudolphi's *G. reptans* which by mistake he called *Anthocephalus macrourus* Rudolphi. In the genus *Anthocephalus* Rudolphi the vesicle is posterior and terminal, and not situated in the neck as it is in the genus *Gymnorhynchus* Rudolphi.

Wagener (1854) also figures a similarly characteristic larva which he too, copying Bremser's mistake, named *A. macrourus*; it is very similar to the one figured by Bremser, but in Wagener's figure the tail-like blastocyst is enormously elongated.

Diesing (1850) erected the genus *Pterobothrium* to accommodate encysted larval tetrarhynchids which had four terminal bothridia arranged in the shape of a cross. He placed four species in the genus, namely:—(1) *Pterobothrium macrourum*

Diesing = " *Anthocephalus macrourus* Rudolphi (*nec* Bremser)" ; (2) *P. crassicolle* Diesing ; (3) *P. heteracanthum* Diesing ; (4) *P. interruptum* Diesing. No type was designated. Later on Diesing figured *P. heteracanthum* with a vesicle in the neck, and he took particular care to point out that his *P. macrourum* was the *A. macrourus* of Rudolphi and not the one figured by Bremser under that name with a vesicle in the neck. In the same paper he also erected the genus *Synbothrium* for an adult tetrarhynchid which had four terminal bothridia arranged in the shape of a cross. The type-species was *S. fragile* Diesing, 1850.

In 1855 he both re-described and figured *P. heteracanthum*. His drawing of this species resembles very closely those given by Bremser and Wagener for *Anthocephalus macrourus*, i. e., for *G. reptans* Rudolphi. The larva differs from all the other known larvæ in that when found in certain species of fishes there is a large globular vesicle situated between the head and the very long tail-like blastocyst. In the same paper Diesing changed the name of his genus *Synbothrium* to *Syndesmobothrium*, and he described and sketched an adult tetrarhynchid having four terminal bothridia arranged in the shape of a cross which he, in 1850, had named *S. fragile*.

Diesing himself called attention to the fact that his two genera *Pterobothrium* and *Synbothrium* were closely related. He says :—" Similar to *Pterobothrium* in the shape of the head, from which it differs, however, in that *Synbothrium* has a segmented body and no receptaculum (vesicle) in the neck."

Vaullegeard (1899) was of opinion that Diesing's figures of *S. fragile* Diesing, 1850, represented the head of the adult worm, whilst Diesing's drawings of *P. heteracanthum* represented the larval stage of the same species.

Diesing (1855) states :—" In my system of Helminths my first described genus *Pterobothrium* would include Rudolphi's species *A. macrourus* and *A. interruptus*. But since Rudolphi did not give a full description of either of his species, I have made the species *P. heteracanthum* the type of my new *Pterobothrium*."

It is thus clear that *P. heteracanthum* is synonymous with Rudolphi's *Gymnorhynchus reptans*, i. e., the *Anthocephalus macrourus* Rudolphi of Bremser and Wagener, especially since Diesing's figure of the larva (*i. e.*, of *P. heteracanthum*) also indicates the presence of the characteristic vesicle similar to that represented by both Bremser and Wagener for *A. macrourus*, i. e., for *G. reptans* Rudolphi.

Syndesmobothrium fragile Diesing, 1850, is undoubtedly the adult form of the larva named by Diesing *P. heteracanthum*, and, in the opinion of the writer, *S. filicolle* Linton, 1899, and *Synbothrium hemuloni* MacCallum, 1921, are also synonymous with *S. fragile* Diesing, 1850.

Vaullegeard (1899) in his account of *Tetrarhynchus fragilis* (Diesing) states that Bremser's figure of the head of *Anthocephalus macrourus* Rud. represents a different worm from that described by Rudolphi under that name. As noted above, Bremser's figures show *Gymnorhynchus reptans* Rudolphi, not *Anthocephalus macrourus* Rudolphi. It is thus clear that the name of the genus is *Gymnorhynchus* Rudolphi, 1819.

Linton (1889) states that the genus *Syndesmobothrium* Diesing, 1855 (= *Gymnorhynchus* Rudolphi, 1819), is characterized by Diesing as follows :—" Body articulate, tæniæform ; neck tubular, rounded at the base ; head tetragonal, with four terminal, prominent bothria attached to head by posterior margin, cruciformly disposed, oval, slightly convex, joined with each other at the base by a membrane ; proboscides four, filiform, armed, each one running through a bothrium (pedicel), excurrent at apex, long, retractile in the neck. Genital apertures marginal (?). In intestines of marine fishes of Tropical America."

The genus is defined as follows :—The head bears four terminal bothridia, usually arranged in the form of a cross, but sometimes pointing anteriorly and without ciliated pits (otocysts). The four proboscides are armed with hooks. The larval form in certain species of fishes is very long, and bears a large characteristic vesicle between the head and the long tail-like blastocyst. In other species of fishes the larval form is simple, consisting of a scolex and a short tail-like blastocyst, the vesicle being absent and the whole larva being enclosed in a simple oval or globular cyst.

Type-species :—*Gymnorhynchus gigas* (Cuvier, 1817).

Key to Species.

Hooks sickle-shaped, in groups of five .... *G. gigas*, p. 152.
Hooks of varying shapes and sizes, not in groups of five .... *G. malleus*, p. 160.

(1) **Gymnorhynchus gigas** (Cuvier, 1817). (Figs. 53 to 56.)

Synonyms :—*Scolex gigas* Cuvier, 1817.
Gymnorhynchus reptans Rudolphi, 1819.
Anthocephalus macrourus Bremser, 1824, and Wagener, 1854.
? *Gymnorhynchus raii* (Rud. ?) Risso, 1826.
Gymnorhynchus horridus Goods., 1841.
Synbothrium fragile Diesing, 1850.
Pterobothrium heteracanthum Diesing, 1850.
Syndesmobothrium fragile Diesing, 1855.
? *Gymnorhynchus elongatus* (Wagener) of Mont., 1893.
Synbothrium filicolle Linton, 1897.
Syndesmobothrium filicolle Linton, 1899.
Tetrarhynchus platycephalus Shipley & Hornell, 1906.
Synbothrium hemuloni MacCallum, 1921.
Vaullegeardia gigas Guiart, 1926.

From (1) *Dasybatus walga*, Pearl Banks, Ceylon. Hornell; Southwell. (2) Larvæ from *Cybium guttatum*, *Chorinemus toloo*, *C. lysan*, *Chirocentrus dorab*, *Serranus* sp., *Balistes* sp., *Lutjanus* sp., *Pristis cuspidatus*, Pearl Banks, Ceylon. Southwell. *Arius gagora* and *Harpodon nehereus*, Delta of Ganges, Bengal, India. Southwell. *Hemigaleus balfouri*, *Trichiurus savala*, *Clupea ilisha*, India. Pearson.

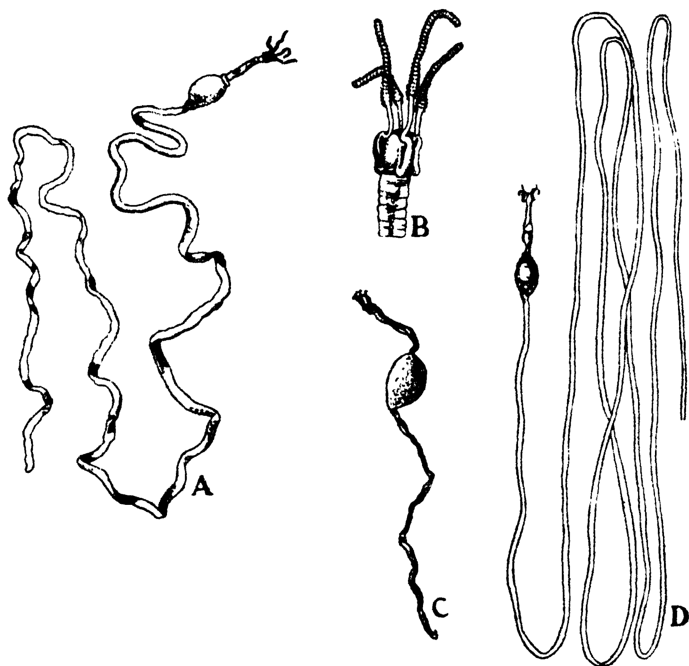


Fig. 53.- *Gymnorhynchus gigas*. A, B - *G. reptans* Rud. (after Bremser); C = *Anthocephalus macrourus* Rud (after Bremser); D = *Anthocephalus macrurus* or *reptans* (after Wagener).

Shipley and Hornell (1906) described *Tetrarhynchus platycephalus* (= *Gymnorhynchus gigas* (Cuvier, 1817)) as follows:—
" This is a moderate-sized form, measuring 10 mm. or 12 mm. in length. The head and neck occupy about one-sixth of the whole body length. The head is compressed from front to back and spreads out laterally, having something like the appearance of a toreador's hat. The four-hooked proboscides bend out towards the edge of the hat, and finally emerge at the angles. The hooks are large, sabre-like, and of uniform size.

"The body consists of ten or eleven segments, the last two of which are as big as the rest of the body altogether. The proglottides are at first some six times as broad as they are long, but the fourth or fifth proglottis is already square, and the last is perhaps four or five times as long as broad. They are rounded and plump, stouter half way along than at either end, and stouter in front than behind. The most characteristic feature is the genital pore. This is a great cleft which runs almost half across the proglottis and seems to half cut it in two. This appears already in the fourth or fifth proglottis, and gives the appearance of an irregular and abnormal segmentation. The pores are lateral and alternate as a rule, though now and then two will consecutively follow each other on the same side.

"The diagnosis of *Tetrarhynchus playcephalus* is as follows:—Head much flattened, proboscides coming out of the edges of the flattened head. Hooks uniform in size, sabre-like. Proglottides ten or eleven in number, broader in the middle than at either end. Reproductive pore resembles a huge cleft which seems to half cut the proglottis in two; alternate but slightly irregular."

Pintner (1913) places this species, together with *Tetrarhynchus rubromaculatus* Shipley & Hornell, 1906, and *Tetrarhynchus benedeni* (=*T. tenuis* van Beneden=*T. gracilis* Diesing), in his genus *Lakistorhynchus*.

As the anatomy of the adult worm has not been fully described, further details are given below.

The worm measures 1·1 cm. in length and the maximum breadth is 360 μ. It is composed of about twelve segments, the last one measuring 2·9 mm. in length and 360 μ in breadth. There is no neck. The genital pores are very large and irregularly alternate, and situated in the posterior third of the segment. They have prominent lips.

Head. The head measures 2·2 mm. in length. Its breadth across the proboscis sacs is 450 μ, across the bothridia 810 μ, and between the sacs and the bothridia the breadth is 360 μ. There are four bothridia, each having a length of 270 μ; their free extremities point anteriorly and their sucking surfaces face towards the median longitudinal axis of the worm. The proboscis sacs measure 900 μ in length and 170 μ in breadth, *i. e.*, they are nearly half the length of the entire head. The sacs are peculiar in that the proboscides can be clearly seen lying coiled within them and extending to the posterior extremity. The proboscides are very short, and within the head are almost straight. Only one of the proboscides was protruded beyond the head; it projected to a length of 90 μ.

Muscular System. The longitudinal muscles are strongly developed and are arranged in fasciæ resembling closely those

found usually amongst the various species of Tænioidea. The nervous and excretory systems were not investigated.

Testes and Vas deferens. The sixth segment is square ; in the seventh there are about 100 well-developed testes ; they are oval, and lie with their long axes transversely. They extend posteriorly to the ovary on both sides and are arranged in two

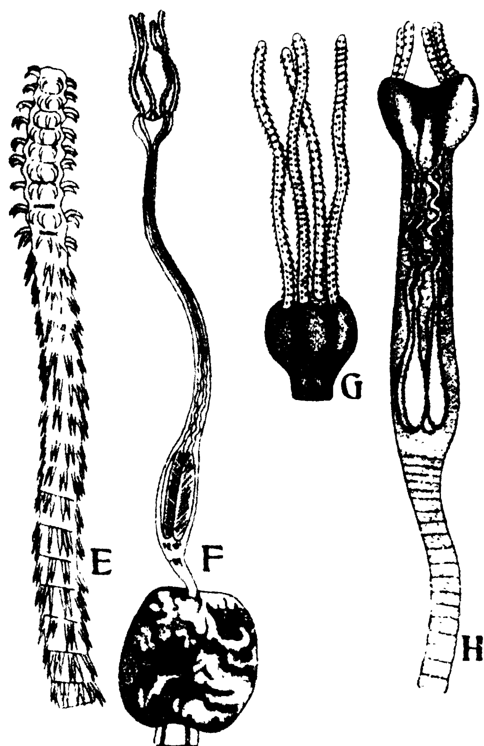


Fig. 54.—*Gymnorhynchus gigas.* E, F = *Pterobothrium heteracanthum* Diesing (after Diesing); G, H = *Syndesmobothrium fragile* Diesing (after Diesing).

groups, one on each side of the median longitudinal axis. The cirrus pouch is very large, globular, and extends more than halfway across the segment. As only one worm was available, details relating to the cirrus and vas deferens could not be obtained. In Shipley and Hornell's specimens the genital pores were very conspicuous. As the writer's specimen was not fully mature, the genital pores were not so prominent as in their worms.

Ovary and Vagina. The ovary is bilobed and situated a little distance from the posterior extremity. Each lobe lies close to the lateral margin of the segment. In total mounts the vagina could not be made out ; but in the last segment its terminal portion was seen to run and open posteriorly to the cirrus pouch.

Vitelline Glands. These are large and prominent, encircling the whole segment, and thus obscuring the genital organs in total mounts. They develop progressively antero-posteriorly.

Uterus. This is a wide sac running along the median longitudinal axis. Anteriorly it turns ventrally and pushes the ventral wall into a vesicle. It seemed clear that later on the wall would rupture at that point.

Eggs. These are oval and measure 43 by 26 μ. They contain a hexacanth embryo and the shell is devoid of filaments.

The writer has obtained numerous larval forms of this parasite from the mesenteries of the species of fish named below, but up to the present the adult worm has only been found twice in India :—

(1) From *Cybium guttatum*. Pearl Banks, Ceylon. Southwell.

Southwell (1912) described the forms thus :—" The head is squarish in front view, with a bothridium at each corner. The bothridia are oval or cup-shaped. The larvæ agree with Linton's figure of this species, save that in the Ceylon specimens the exits of the proboscides were closed. The proboscis sacs were marked with fine criss-cross lines, only visible under high magnifications." It is practically certain that one of the larvæ described by Shipley an Hornell (1906) from this host (viz., pl. iii, fig. 43) belongs to the same species.

(2) From *Chorinemus toloo* and *C. lysan*, Pearl Banks, Ceylon. Southwell.

The cysts which occur in this fish are quite unlike those found in *Chirocentrus dorab* and *Hemigaleus balfouri* (v. inf. p. 158); they are somewhat tadpole-shaped, having a length of about 1·2 cm. The cyst has a breadth of about 1 mm., whilst the tadpole-like head of the cyst containing the larva measures 2 mm. in length and 1·5 mm. in breadth. A description of this larva is given by Southwell (1912).

(3) From *Arius gagora*. Sunderbans (Delta of the Ganges), Bengal, India. Southwell.

The cysts are very long, milky white in colour, and tadpole-shaped, measuring from 3 to 4 cm. in length and 2 to 3 mm. in breadth. The " head " of the cyst which contains the larva measures 4·5 mm. in length and 2·5 mm. in breadth. There is a slight constriction between the " head " and the rest of the cyst. The larva itself lies " tied in knots " within the " head " of the cyst ; the blastocyst, to which the head of the worm is attached, measures 2 cm. in length and 700 μ

in breadth. The head measures about 4 mm. in length and has a maximum breadth of about 500 μ.

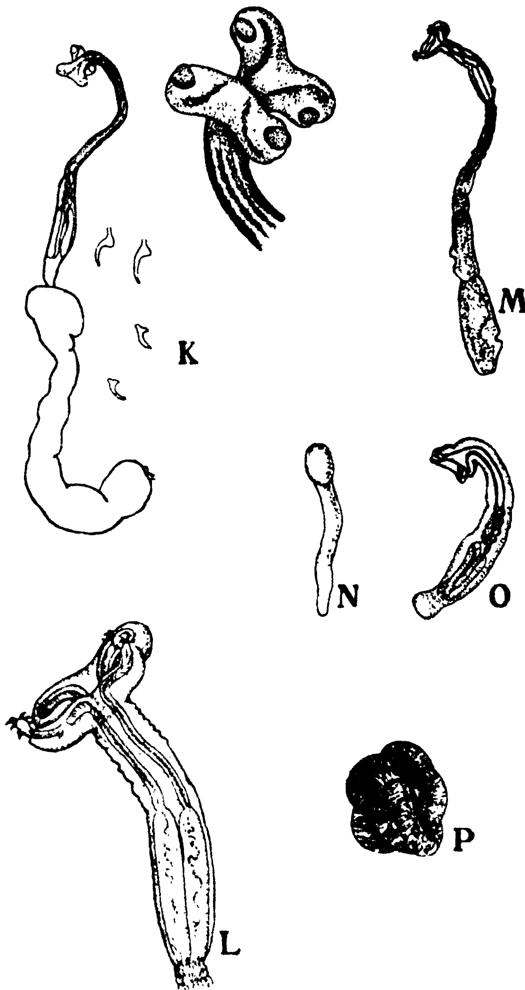


Fig. 55. *Gymnorhynchus gigas.* K = *Syndesmobothrium filicolle* Lint. (after Linton); L, M *Tetrarhynchus platycephalus* Shipley & Hornell (after Shipley and Hornell); N, O *Syndesmobothrium filicolle* Lint., cyst and larva (after Southwell); P, larva from *Arius gagora*, × 10 (after Southwell).

The free unencysted larva and its attached blastocyst presented very extraordinary characteristics. It measured

6 cm. in length; the anterior portion was hair-like, and it gradually broadened until the extreme posterior portion had a breadth of 700 μ. There is no doubt that in this larva both the head and the blastocyst had elongated to about three times their original lengths. It is interesting to note that Wagener (1854) figures (pl. xvi, fig. 212) a very similar condition in the larva of "*Anthocephalus macrurus* (sic *macrourus*) oder *reptans*" obtained from *Brama raji*.

The head of the worm measured 10 mm. in length and the proboscis sacs 1·6 mm. in length. The breadth across the bothridia was 340 μ and across the proboscis sacs 200 μ. The diameter of that portion of the head between the bothridia and the proboscis sacs is 72 μ only. The proboscides and their sheaths had elongated so as to resemble hairs. The whole condition is artificial, due to extreme elongation, a phenomenon which the writer has noticed before whilst examining living worms of other species on the Pearl Banks. The proboscides were everted and the hooks were exactly similar to those figured for the same species found under No. 4 below.

(4) From (*a*) *Chirocentrus dorab*, Pearl Banks, Ceylon. Southwell. (*b*) *Hemigaleus balfouri*, Manapad, Tinnevelly Dist., S. India. Pearson.

The cyst in these two hosts is of a most unusual shape. Posteriorly there is a long tail-like portion, measuring about 10 mm. in length and 600 μ in breadth, which anteriorly expands into a perfectly globular thin-walled vesicle having a diameter of 2 mm. From the latter the head proper arises.

Bremser (1824) on pl. xi, fig. 11, gives a picture of *Gymnorhynchus reptans* showing the vesicle in question; and on pl. xvii, fig. 1, he figures in mistake a very similar condition of the cystic form in *Antocephalus* (sic *Anthocephalus*) *macrourus* Rudolphi, 1819 = *Gymnorhynchus reptans* Rud., 1819 = *G. gigas* Cuvier, 1817).

The complete head measures 3·8 mm. in length; its breadth across the proboscis is 360 μ, across the bothridia 630 μ, and between the two it has a breadth of 200 μ. There are four very small bothridia each forming an angle of about 45 degrees with the long axis of the worm, and each having the sucking surface facing the median longitudinal axis of the worm. Each bothridium has a length of about 300 μ. The proboscis sacs have a length of 900 μ, that is, they are about one-quarter the length of the head. Within the posterior part of the head the proboscides are much coiled, but in the anterior part they run a straight course. The free portion of the proboscides (*i. e.*, the part of the proboscides protruded beyond the head) is almost equal to half the length of the head. The hooks on the proboscides are diagnostic; they arise in clusters of about five on each side, a bunch of five on one side being

situated midway between two sets of five on the other side. Superficially only three hooks can be seen in each group; by deep focussing five are visible; the bases of all the five

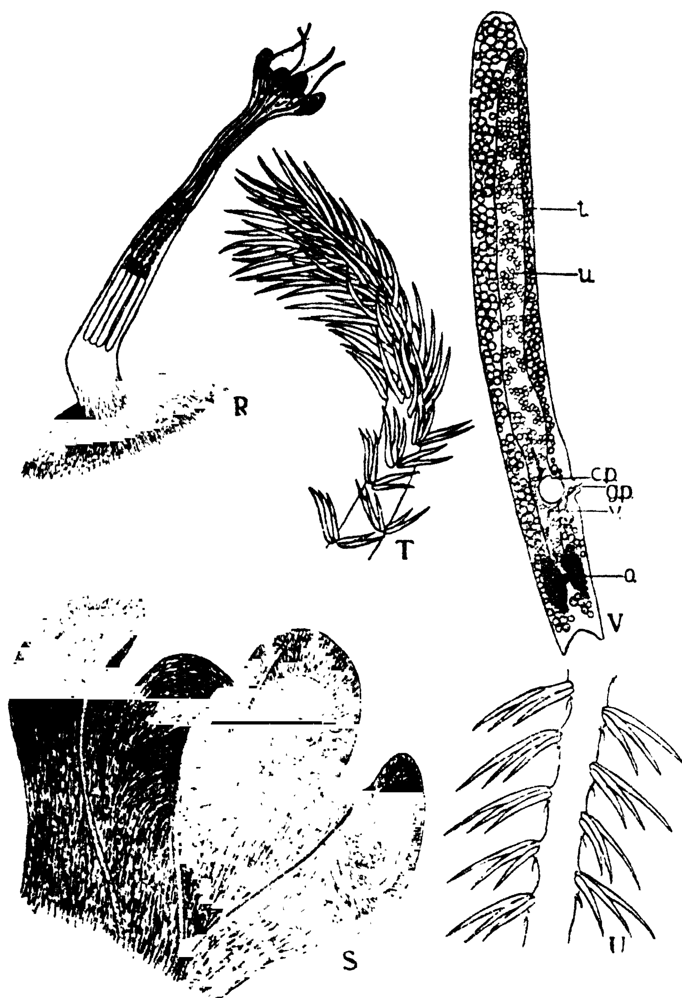


Fig. 56.—*Gymnorhynchus gigas*. R, head and vesicle (receptaculum). × 15; S, the four bothridia, × 160; T, anterior extremity of proboscis, 160; U, another portion of proboscis, × 160; V, partly gravid segment, × 160. (After Southwell.)

hooks in each cluster are close together. The hooks in each group vary in size, the largest measuring about 110 μ and the smallest 70 μ. They are all delicate. Posteriorly to each

set of five there is a very small hook measuring 17 μ. At their anterior extremities the proboscides are armed with long hooks arranged closely together and with their points directed anteriorly so as to resemble a shaving brush.

(5) From the mesentery of *Trichiurus savala*, seas and estuaries of India; and *Clupea ilisha*, Indian Ocean, ascending large rivers. Pearson.

(6) From *Serranus* sp., *Balistes* sp., and *Lutjanus* sp., Pearl Banks, Ceylon. Southwell.

(7) From liver and mesentery of *Pristis cuspidatus*, Pearl Banks, Ceylon. Southwell.

(2) **Gymnorhynchus malleus** (Linton, 1924). (Figs. 57 & 58.)

Synonyms:—*Synbothrium malleum* Linton, 1924.
Tetrarhynchus erinaceus Linton, 1897.

From (1) *Pteroplatea micrura*, Pearl Banks. Pearson. (2) *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

Linton in 1905 described and figured another member of this genus—a larval form—from various species of fish. This parasite has peculiar hooks, and he referred to it as *Synbothrium* sp. His description was as follows:—" 1901, July 11: One cestode larva, which is probably to be referred to this species. The cyst was found in the liver, and measured 25 mm. in length and 3 mm. in diameter. The blastocyst was about the same size as the enveloping cyst and was very active. When flattened, marginal sinuous vessels were seen, but no appearance of a larva. The killed specimen measured 14 mm. in length. July 12: a cyst similar to the foregoing found on this date yielded a larva which appears to belong to this species. Dimensions, in millimetres: Length 6; breadth of head 1·2; diameter of neck 0·6; length of contractile bulbs 1, diameter 0·27; diameter of proboscis, exclusive of hooks, 0·1. Specimen somewhat compressed."

In 1924 Linton described the adult specimen, viz., *Synbothrium malleum* Linton, 1924, from *Dasybatus centrurus*, concluding that the larval forms noted above belonged to this new species. He called attention to the fact that the hooks of his *S. malleum* bore a close resemblance both in size and arrangement to those of *Tetrarhynchus erinaceus*. The resemblance is indeed remarkable, but in other respects the heads of the two species in question are entirely different. In fact, Linton had named and figured the same larva as *T. erinaceus* in 1897.

The largest worm examined by the writer measured about 6 cm. and contained 47 segments. The greatest breadth was 1·5 mm. There was no neck. The eighteenth segment was square, measuring 700 μ. The last segment contained numerous eggs and measured 1·85 mm. in length and 1·45 mm. in breadth.

The genital pores are irregularly alternate and situated laterally at the base of a deep pit in the posterior third of the segment. Eggs appear suddenly; they are entirely absent in one segment and very abundant in the suoceeding one. They

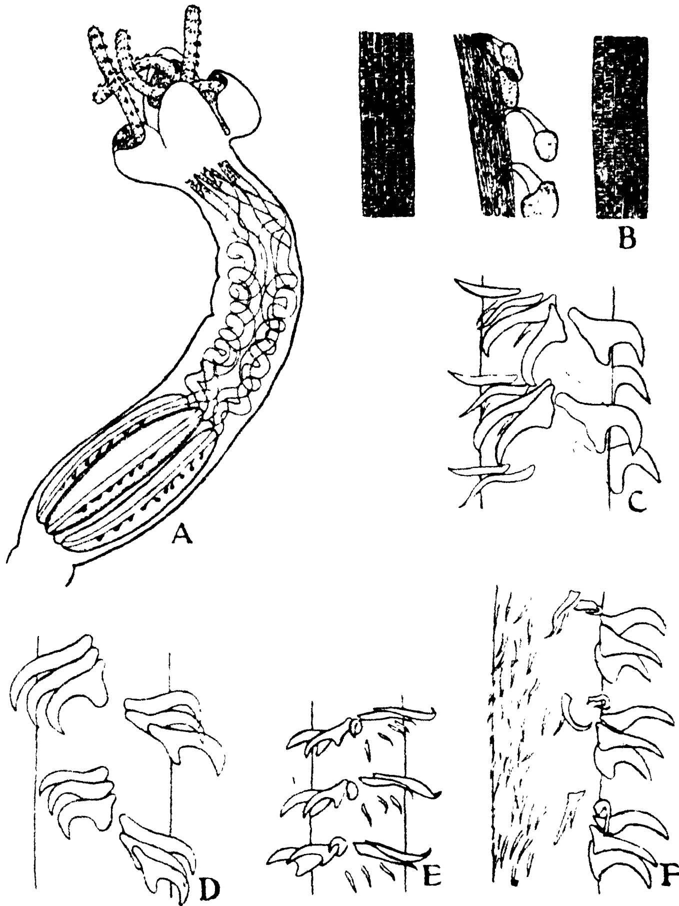


Fig. 57.—*Gymnorhynchus malleus.* A, head, × 35; B, proboscis sac, showing "granular bodies" attached to small bundles of muscle fibres, × 155; C, D, proboscis hooks, × 250; E, F, proboscis hooks, basal, × 160. (After Southwell.)

occurred in the last twelve segments of the largest worm. Under low magnification the outstanding characters of this worm are:—(1) the longitudinal lines in which the muscle fibres and the vitelline glands are arranged in the mature and

gravid segments; (2) the sudden disappearance of the thick uterine wall and the loose appearance of the eggs; (3) the arrangements of the hooks on the proboscides.

Head. This measures 5 mm. in length; its breadth is as follows: anteriorly across the bothridia 1·26 mm.; across the proboscis sacs 950 μ, between the bothridia and the proboscis sacs 750 μ. There are four small sucker-like bothridia facing anteriorly, each having a diameter of about 400 μ. The proboscis sacs have a length of 1·8 mm. and a breadth of 220 μ. Within the head the proboscides are much coiled, but their free portion is very short. The hooks on the proboscides are characteristic of the species; they have the form and arrangement shown in fig. 57.

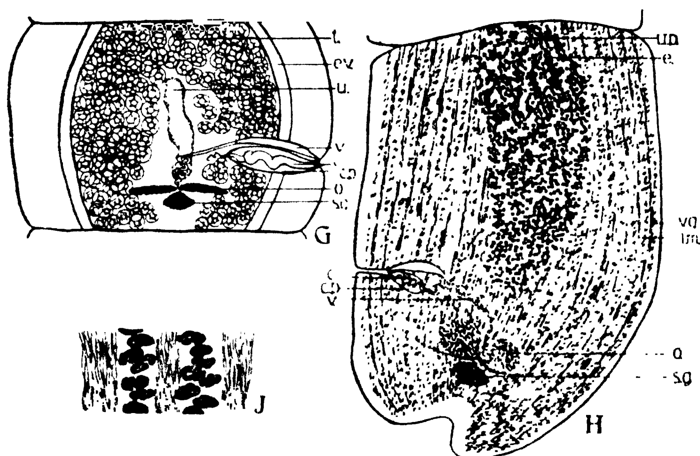


Fig. 58.—*Gymnorhynchus malleus.* G, mature segment, × 56; H, nearly gravid segment, × 33; J, diagram showing disposition of vitellaria and longitudinal muscles, × 250. (After Southwell.)

Rudiments of the ovary, vagina, uterus, and vas deferens are prominent in the third or fourth segment.

Testes and Vas deferens. In stained total mounts the testes can be seen only in two or three segments, and even then with difficulty, owing to the fact that the vitelline glands develop simultaneously and obscure them. They are fairly numerous (about 200), and extend posteriorly on each side of the segment to the ovary. In the fully mature proglottides the cirrus pouch has a length of 720 μ, and a breadth of 380 μ; the cirrus is unarmed, and lies in several coils within the pouch. Outside the sac its course is very short.

Ovary and Vagina. The ovary is bilobed, finely granular, and situated posteriorly. The vagina in young segments is much coiled; it opens slightly anteriorly and dorsally to the cirrus

pouch into the deep pit noted above. No seminal vesicle was seen, but just median to the genital opening the vagina dilates into a wide sac.

Vitelline Glands. These extend over the whole of the dorsal and ventral surface of the segment. They are very markedly developed, even in the immature segments, and lie between the bundles of longitudinal muscle fibres. Posteriorly a duct arises laterally from each side, and these unite in the median line and open into the fertilization canal.

Shell Gland. This is a conspicuous organ situated behind and between the two wings of the ovary, and has a fan-shaped appearance.

Uterus. The uterus in a gravid segment is remarkable. Eggs are absent in one segment and very numerous in the next. It appears to be a central cavity devoid of a proper wall. In immature segments it, as usual, appears as a central stem with a thick (? glandular) wall, but the moment eggs can be seen this stout membrane disappears and the eggs seem to be loose and unconfined in the central parenchyma. At the anterior margin of the gravid segment in the longitudinal axis there is a ventral uterine pore.

Eggs. The egg measures 45 by 21 μ and does not bear filaments. No details relating to its contents could be made out.

Genus IV. **OTOBOTHRIUM** Linton, 1890.

Linton defined the characters of this genus as follows :— " Body articulate, tæniæform, head separated from the body by a neck. Bothridia two, opposite, lateral, each with two supplemental ciliated pits at the posterior free angles. Proboscides four, terminal, filiform, armed, retractile in neck. Reproductive apertures marginal." These characters have been emended as follows, to accommodate *O. balli* Southwell, 1929, in which the supplemental ciliated pits are situated in the middle of the margin of the bothridia, and *O. dipsacum* Linton, 1897, in which there are four bothridia :—

The head bears either two opposite lateral bothridia, each with two supplemental ciliated pits, or it bears four bothridia, each with a single ciliated pit.

Type-species :—*Otobothrium crenacolle* Linton, 1890.

Six species have been identified, three of which have been recorded from India and Ceylon.

Key to Species.

1.	With four bothridia	*O. dipsacum*, p. 165.
	With two bothridia	2.
2.	Hooks on proboscis all small, 18 μ or less, and practically alike	*O. balli*, p. 166.
	Hooks of various shapes and sizes	*O. linstowi*, p. 164.

(1) Otobothrium linstowi Southwell, 1912. (Fig. 59.)

Synonym:—*Otobothrium magnum* Southwell, 1924.

From *Pristis cuspidatus* and *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Southwell.

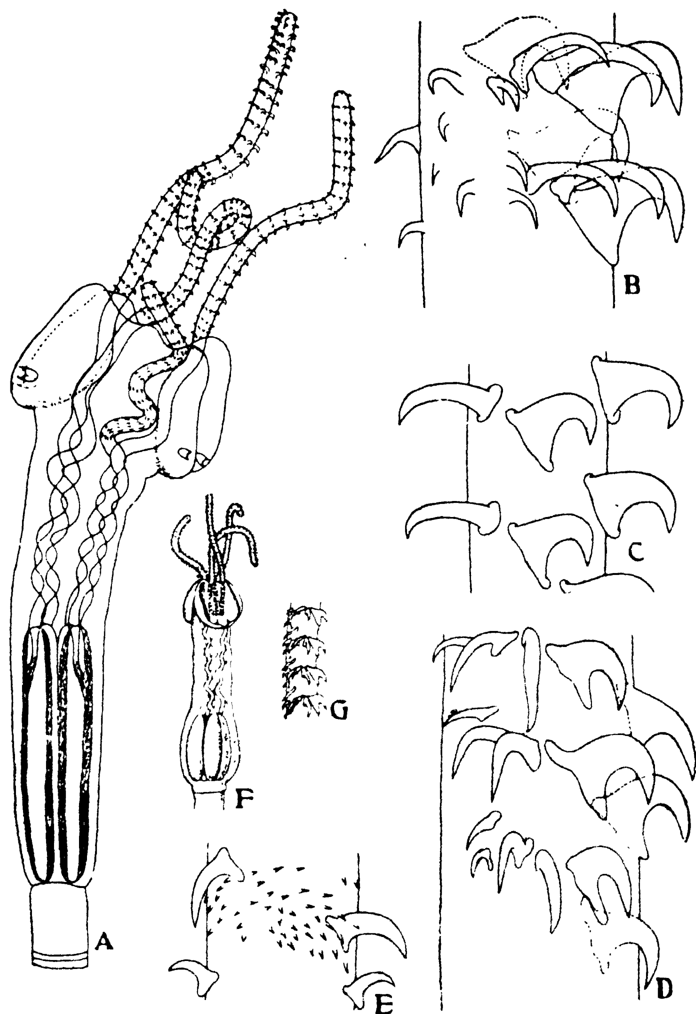


Fig. 59.—*Otobothrium linstowi.* A, head, ×46; B, C, D, E, proboscis hooks, × 214; F, head, × 10; G, hooks, magnification unknown. (After Southwell.)

Adult worms 3·5 cm. in length, with a maximum breadth of 500 μ and composed of about 50 segments. The head

measures from 4 to 4·5 mm. in length and has a maximum breadth of 1·3 mm. The two bothridia each have a length of 1 mm. and the proboscis sacs measure 1·75 mm., viz. about one-third the length of the entire head. The hooks on the proboscides are spirally arranged on one face only; on the opposite face they are irregularly disposed; they are of various shapes and sizes, as shown in fig. 59. One face of each proboscis bears spiral rows of large dissimilar hooks, there being from three to five hooks in each row; the other face has a number of small delicate hooks of various shapes and sizes arranged quite irregularly. The largest hooks have a length of 80 μ and the smaller ones 20 μ. Towards the tip of the proboscis *all* the hooks decrease in size gradually. The base of each proboscis is not swollen, but it bears a cluster of extremely small and delicate spines measuring about 9 μ in length.

Larval Forms.

(2) **Otobothrium dipsacum** Linton, 1897. (Fig. 60.)

Synonym :—*Otobothrium insigne* Southwell, 1912.

From (1) *Serranus undulosus*, Pearl Banks, Ceylon. Southwell. (2) *Diagramma crassispinum*, *Balistes mitis*, *Lutjanus dodecacanthus*, and *Lethrinus ornatus*, Pearl Banks, Ceylon. Pearson.

The cyst measures 1·2 cm. by 6 mm. and contains a pear-shaped blastocyst 8·5 mm. in length, 6 mm. in diameter at the broader end, and tapering to a blunt point posteriorly. The larva measures about 5 mm. in length. There are four bothridia, each with a ciliated pit posteriorly. The arrangement of the hooks is characteristic of the species. On each proboscis there is a longitudinal line towards which the shorter diagonal rows of hooks converge on each side. The longest measures 50 μ.

It will be noted that in the original description of the genus Linton stated that there are two bothridia only. In *O. dipsacum* he said that there are four, and this is actually so. But it is clear that each lateral half of the head, with its two marginal bothridia, forms one complete sucker and acts as a single bothridium.

The cysts are club-shaped and measure up to 4 cm. in length; the maximum breadth is about 6 mm. The fully developed cysts are dense jet-black with very firm walls. Very young cysts are not pigmented. All stages between the two conditions are to be seen.

The larvæ, attached by their heads to one end of the cysts, have a length of 3 or 4 mm. The four bothridia are in pairs; each measures about 1 mm. and bears near its posterior

extremity a ciliated sucker-like sac or pit having a diameter of 120 μ. The hooks are slender and nearly all of the same shape, the longest measuring 47 and the shortest 14 μ. The characteristic arrangement of the hooks described by Linton was very pronounced in our specimens.

Southwell (1912) identified these larvæ as *O. insigne* Linton, 1905. A re-examination of the hooks proved them to be *O. dipsacum* Linton, 1897.

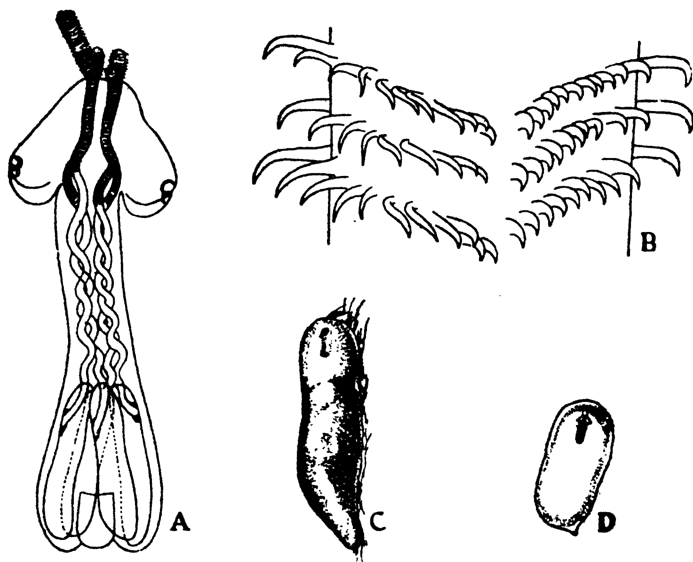


Fig. 60.—*Otobothrium dipsacum.* A, larva, × 24; B, proboscis hooks, × 330; C, D = *O. insigne* Southwell, 1912: cysts, magnification unknown. (After Southwell.)

(3) **Otobothrium balli** Southwell, 1929. (Fig. 61.)

Larval forms from (1) *Cybium guttatum*, *Lethrinus ornatus*, and *Balistes stellatus*, Pearl Banks, Ceylon. Southwell. (2) *Aprion pristipoma*, Negapatam, Tanjore Dist., S. India. Pearson.

The cysts in *Aprion pristipoma* are oval and milky white and measured 7 by 4 mm. The inner cyst is 5 by 2·5 mm. The larva, to which no blastocyst is attached, measures about 1·7 mm. in length and has a maximum breadth of about 1·1 mm. There are two bothridia each having a length of 900 μ, *i. e.*, more than half the length of the head. They each bear two ciliated pits situated one along each lateral margin, but instead of being posterior they are slightly

nearer the anterior extremity of the bothridia than the posterior. The proboscis sacs are oval, having a length of 350 μ and a breadth of 100 μ. Their anterior extremities are overhung by the posterior part of the bothridia. The proboscides are very short and lie almost straight within the

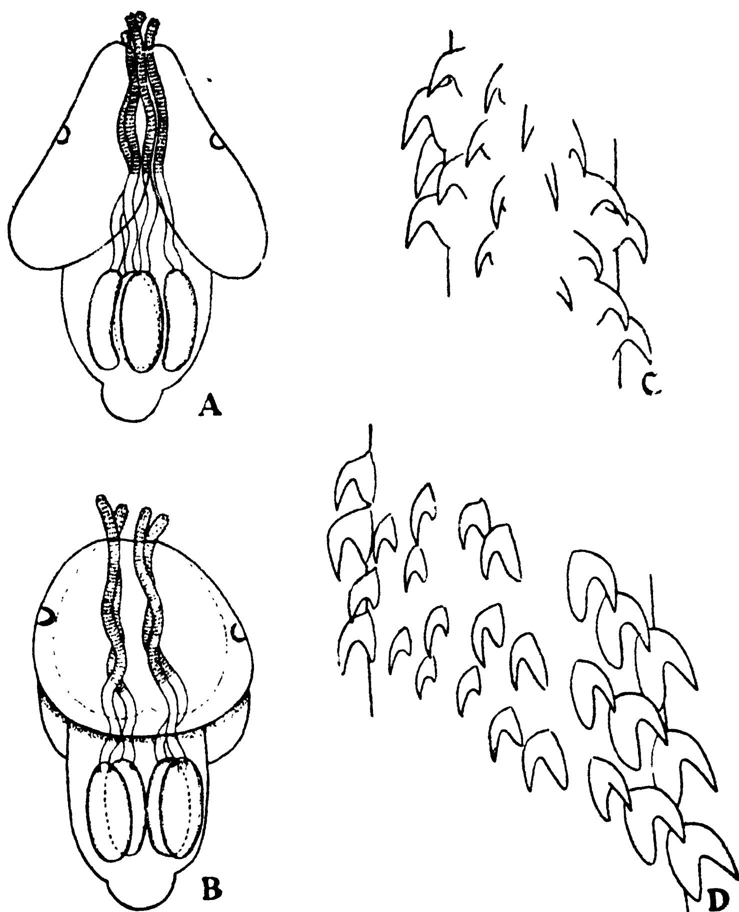


Fig. 61.—*Otobothrium balli.* A, larva, lateral view; B, larva, dorso-ventral view, × 35; C, D, proboscis hooks, × 500. (After Southwell.)

head. They are armed with small, curved, almost uniform hooks having a rather stout base and arranged spirally. These vary in size from about 8 to 18 μ, and are densely crowded together.

Larval Forms of uncertain Generic Position.

A.—Tetrarhynchus spp (Figs. 62 & 63.)

(1) and (2). Shipley and Hornell described two different tetrarhynchid larvæ from *Cybium guttatum*, Pearl Banks, Ceylon. One was encysted, the other was free.

The first species occurs in voluminous cysts, each measuring

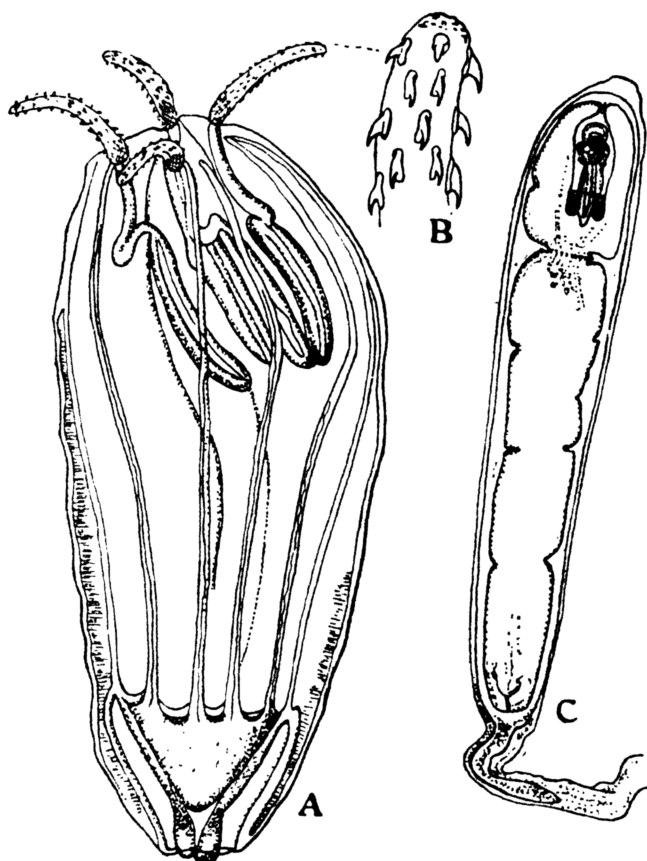


Fig. 62.—*Tetrarhynchus* sp. From *Cybium guttatum*. A, larva, × 25; B, proboscis hooks; C, cyst, magnification unknown. (After Shipley and Hornell.)

up to 1·4 cm. in length and having a breadth of 2·5 mm. They are found in the body cavity. The larval head is much smaller than the one described below; it is invaginated, and the walls of the cavity in which it lies meet and all but fuse. They are then continued backwards as the wall of the cyst, which is

contracted here and there. Posteriorly the exit of the excretory system is visible.

The one without a cyst is egg-shaped, measuring 4 mm. in length, and having a maximum breadth of 2 mm. The "tail or posterior end is ensheathed in a circular fold like a petticoat, and from it runs up a number of ribs or ridges which fade out in the head. The teeth on the proboscides are large and stout, and comparatively sparse."

(3) It is impossible to identify the larval tetrarhynchids mentioned by Shipley and Hornell, 1906, found in *Chirocentrus dorab* (fig. 63), *Lutjanus annularis*, *Diagramma* sp., and *Sphyræna commersoni*. It seems probable that those found in the last-named host are *Gymnorhynchus gigas* (Cuvier, 1817).

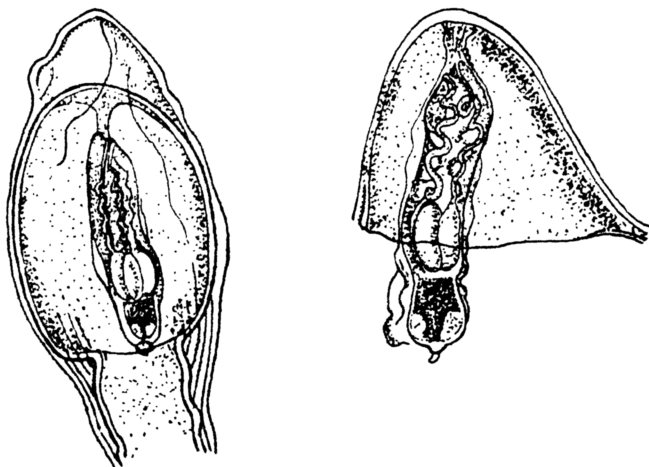


Fig. 63.—Tetrarhynchid cyst. From *Chirocentrus dorab*; magnification unknown. (After Shipley and Hornell.)

(4) Meggitt (1927) records a tetrarhynchid larva from a snake (*Hurria rhynchops*) in Burma, and Moghe (1926) a larval tetrarhynchid from *Barbus sophore* in India.

(5) A collection of ten tetrarhynchid cysts from the mesenteries of *Balistes mitis*, *Balistes stellatus*, *Lutjanus* sp., and *Serranus undulosus*, Pearl Banks, Ceylon, was examined. The cysts were roughly oval, milky white or light brown, and measured 10 by 3 mm. An unidentified larval nematode about 1 to 1·2 cm. in length was found attached to the outer cyst wall in every case, and in each instance the cestode larva within the cyst had degenerated into a brownish unrecognizable mass.

B.—Plerocercoid larva I. (Fig. 64.)

(=*Ilisha parthenogenetica* Southwell & Prashad, 1918.)

From *Clupea ilisha*, Khulna, Bengal, India. Southwell.

When describing this parasite in 1918 it was believed that the worm was an adult degenerate cestode which was peculiar in having a special method of reproduction—namely, by parthenogenesis. The author has recently re-examined the



Fig. 64.— Plerocercoid larva I, magnification unknown. (After Southwell and Prashad.)

original and some fresh material, and has again fully considered, in view of this further work, whether the conclusions then arrived at were justified.

The method of reproduction exhibited by this worm is very similar to the elaboration of the germ-balls in the sporocysts of trematodes like *Fasciola hepatica.* The resemblance, however, is purely superficial, for whereas in *I. parthenogenetica* the parthenogenetic development leads directly to the production

of forms exactly similar to the parent, in the trematode the asexual reproduction results in the formation of rediæ, and finally of cercariæ, both of which are very different from the sporocyst in which they are produced.

The exact manner in which endogenous embryos arise in the larval cestodes described by Hornell (1906), Willey (1907), and Southwell (1910) is not known, as in all these instances the larvæ were fully developed, and in no case had the intermediate stages been observed. In the parasite of the Indian shad, however, it was possible to study the development of the parthenogenetically developed forms. The method detailed by the authors referred to above does not materially differ from what occurs in *I. parthenogenetica*, and accordingly it is clear that the parasite of the Indian shad is not an adult degenerate cestode but a plerocercoid larva, the adult of which is unknown.

The larvæ described by Hornell, Willey, and Southwell were found in the Pearl Oyster (*Margaritifera vulgaris* Linn.) and the Window-pane Oyster (*Placuna placenta* Linn.) of Ceylon. Haswell and Hill (1894) had previously obtained a similar worm, with an identical mode of reproduction, from an Australian earthworm. The only two other instances of the occurrence of such asexual modes of reproduction in the cestode parasites of the vertebrates are those described by Ijima (1905) and Beddard (1912). The parasite of the Indian shad provides the first instance of endogenous reproduction taking place in a plerocercoid form parasitic in any fish.

Plerocercoid larva II, Southwell, 1921. (Fig. 65.)

From the umbrella of a rhizostomous medusa (*Acromitus rabanchatu*), Barkuda Island, Chilka Lake, India. Annandale.

The larvæ are cylindrical, with broad, rounded extremities, and they measure from 2 to 2·5 mm. in length; the diameter is 340 μ (fig. 65 A and B). They lie in cavities in the host, but are not surrounded by a definite adventitious cyst, although there is a slightly marked condensation of host-tissue round them. Both fresh and preserved specimens have a milky white colour, and can be seen easily with the naked eye, especially in the fresh condition. The larva is solid, and is covered with a conspicuous cuticle. There is a very definite subcuticular tissue made up of a series of small spindle-shaped cells, closely packed together, the nuclei of which stain deeply. Internally the larva consists of a stroma framework enclosing a few large cells which in cross-section measure about 38 by 25 μ. These cells are at first granular, but later on calcareous corpuscles develop and gradually fill them. Eventually the calcareous corpuscles (which are very large and numerous) become free, and the cells which secreted them

are no longer visible, having been replaced by others apparently from the subcuticular layer.

The anterior extremity is marked by a deep pit lined with extremely small spines. The base of this pit is thickened, the proliferating tissue consisting of very numerous, small, elongated cells with well defined nuclei. As in many other Cestoda, the head arises from the base of this pit. In our specimens development had not proceeded beyond the formation of the pit, and no trace of the head was to be seen. The differences

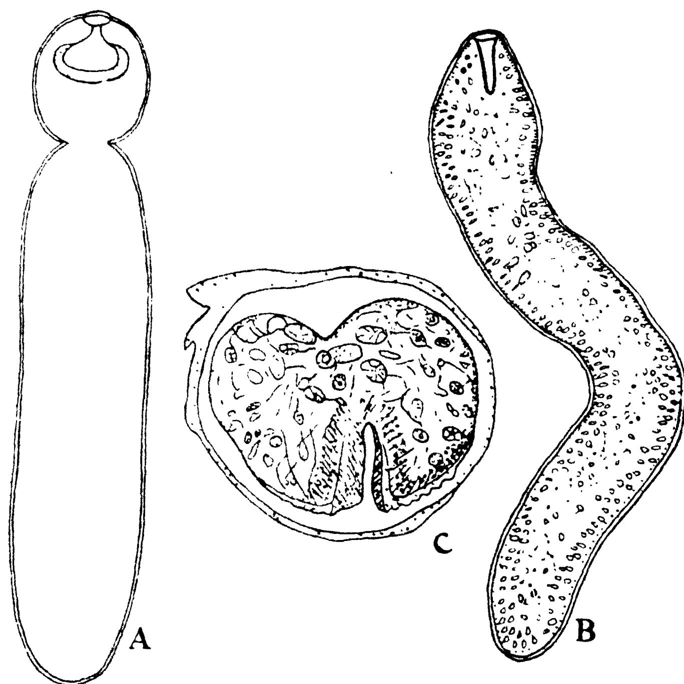


Fig. 65.—Plerocercoid larva II. From Jelly-fish. A, B, ×69; C, transverse section, × 143. (After Southwell.)

noted in the specimens were confined to the size and shape of the pit. In one or two instances a constriction appeared immediately behind the rudimentary head, separating the worm into two parts (fig. 65 A).

There can be no doubt that the parasites are plerocercoid larvæ. It is impossible to identify them at this stage of their development.

As far as the writer is aware, no cestode larvæ have been recorded previously from animals so low in the zoological scale as Medusæ.

Superfamily III. PHYLLOBOTHRIOIDEA, nov.

Synonym :—Order Tetraphyllidea Carus, 1863.

Abildgaard (1790) under the name *Tænia corollata* described a worm with an armed head found in *Raja batis* and *Squalus spinax*.

We have noted elsewhere that Rudolphi in 1809 erected the genus *Bothriocephalus*. In 1810 he divided the species of this genus into two groups, viz., (*a*) Inermes, *Gymnobothria*, and (*b*) Armati, *Echinobothria*. He placed *Tænia corollata* Abildgaard, 1790 (=*Halysis corollata* Zeder, 1803), in the latter division. In 1819 he changed the name of the species to *Bothriocephalus coronatus*, and in the same year described two other species with armed heads from *Squalus galeus*, viz., *Bothriocephalus uncinatus* and *B. verticillatus*. These three species are now known as *Acanthobothrium coronatum*, *A. uncinatum*, and *Calliobothrium verticillatum* respectively.

Dujardin (1845) followed Rudolphi in placing the above three species amongst the armed bothriocephalids.

It has already been pointed out that van Beneden (1850) divided the Cestoda into four orders, one of which he named Tetraphylles. In this order he placed three families, with the following genera, viz. :—

(1) Phyllobothriens : *Echeneibothrium* van Beneden, 1850 ; *Phyllobothrium* van Beneden, 1850 ; *Anthobothrium* van Beneden, 1850.

(2) Phyllacanthiens : *Acanthobothrium* van Beneden, 1850 ; *Onchobothrium* Blainville, 1828 ; *Calliobothrium* van Beneden, 1850.

(3) Phyllorhynchiens : *Tetrarhynchus* Rudolphi, 1809.

It will be noted that this author erected five new genera.

Carus (1863) accepted van Beneden's classification of this family, and he defined it as follows :—" The anterior extremity of the scolex carries four bothridia, either sessile or pedunculated, very mobile, and either armed or unarmed ; the bothridia are sometimes united in pairs ; behind the head there is a chain of segments which contain the genital organs ; this family is found principally in rays."

Braun (1894–1900) defined the order Tetraphyllidea Carus, 1863, thus :—" Scolex armed or unarmed ; with four mobile, pedunculated or sessile bothridia, whose surface may be divided up into areolæ, or which may bear four suckers ; the head may also present an irregular appearance, and may be surrounded with a terminal sucker ; a pseudoscolex is sometimes present. Neck present or absent. Segmentation

distinct; frequently the segments become detached before the chain is fully developed, and they live a free existence in the intestine of the host; no primary uterine pore; cirrus and vagina always open marginally; testes in the medulla, and numerous; yolk glands in two lateral strips in the cortical parenchyma; ovary usually bilobed; shell gland situated behind the ovary; an egg-swallowing apparatus present. Eggs usually thin-shelled and either spindle-shaped or round, sometimes with filaments, but without operculum. Larva described as 'Scolex' by Müller. Found in fish, amphibians and reptiles."

He divided the order into the following four families, viz.:—

(1) Onchobothriidæ Braun, 1900 = Phyllacanthiens van Beneden, 1850.
(2) Phyllobothriidæ Braun, 1900 = Phyllobothriens van Beneden, 1850.
(3) Lecanicephalidæ Braun, 1900 = Gamobothriidæ Linton, 1889.
(4) Ichthyotæniidæ Ariola, 1899.

Meggitt (1924) divided the order into five families, viz.:—

(1) Phyllobothriidæ; (2) Onchobothriidæ; (3) Lecanicephalidæ; (4) Ichthyotæniidæ; (5) Polypocephalidæ.

Poche (1926) divided his subsubclass Tænioinei into four orders, one of which he named Tæniidea; it contained two suborders, viz., (1) Phyllobothriinæ (including the families Onchobothriidæ, Phyllobothriidæ, Lecanicephalidæ, Proteocephalidæ, Monticelliidæ, and Polypocephalidæ), and (2) Tæniinæ.

Woodland (1927) united the orders Trypanorhyncha and Tetraphyllidea, together with the family Proteocephalidæ, into one order, for which he retained the name Tetraphyllidea. In this order he recognized three families, viz., (1) Phyllobothriidæ (sens. nov.) (including, with or without distinction, the old families Phyllobothriidæ and Onchobothriidæ, (2) Proteocephalidæ, and (3) Tetrarhynchidæ (=Trypanorhyncha).

Pintner (1928) does not recognize the order Tetraphyllidea, but he includes the following families, along with others, in his order Cestodes, s. str., viz., (1) Tetraphyllidæ (presumably including the old families Phyllobothriidæ and Onchobothriidæ), (2) Proteocephalidæ (=Ichthyotæniidæ). He split the family Lecanicephalidæ Braun, 1900, into three new families, viz., (3) Tetragonocephalidæ, (4) Cephalobothriidæ, (5) Balanobothriidæ.

For a fuller account of the history of this order, see Southwell, 1925. In this volume the superfamily is divided into two families, viz., Phyllobothriidæ and Onchobothriidæ, and two new superfamilies are erected for the two families Lecanicephalidæ and Proteocephalidæ.

Superfamily III. Phyllobothrioidea, nov.

Synonyms:—Section Tétraphyllides van Ben., 1849.
Section Tétraphylles van Ben., 1850.
Family Tetraphyllidea Carus, 1863.
Order Tetraphyllidea Lühe, 1910, *pro parte.*

Scolex armed or unarmed, composed of very mobile bothridia, which are either sessile or pedunculated, and which may have their surfaces split up into areolæ, with or without accessory suckers. The head may also bear a terminal sucker; a pseudoscolex may be present in addition to a scolex; neck present or absent. Strobila definitely segmented; usually segments are shed before they are fully ripe, in which case they ripen and become gravid in the intestine of the host. Genital pores marginal.

The longitudinal muscles either occupy varying proportions of the cortical parenchyma in the form of rather large compact bundles or are feebly developed, the separate fibres being scattered irregularly in the cortical tissue. A primary uterine pore, situated ventrally, is usually absent but may be present; a secondary uterine pore, or pores, due to atrophy of the ventral body wall leading to dehiscence, occurs in some species in which true uterine pores are absent. Vitelline glands in two lateral fields, occasionally extending across the whole surface of the segment, situated in front of the ovary, but portions sometimes extend posteriorly to it. Ovary butterfly-shaped superficially; egg-swallowing apparatus usually present. Shell gland posterior, usually situated between the lobes of the ovary. Eggs thin-shelled, not operculated, spindle-shaped or round, often with filaments. Parasitic in elasmobranchs.

Key to Families.

Scolex unarmed	**Phyllobothriidæ**, p. 175.
Scolex armed with hooks	**Onchobothriidæ**, p. 234.

Family I. PHYLLOBOTHRIIDÆ Braun, 1900.

Synonym:—Tribe *Phyllobothriens* van Ben., 1850.

Van Beneden defined this tribe as follows:—"The bothridia are fleshy (soft) and do not possess anything in the nature of hooks or spines. The genera are based on the modification of the bothridia, the absence, presence, or the form of the hooks." It is to be noticed that the latter part of van Beneden's statement is curiously at variance with the former part, as the bothridia in this tribe or family are unarmed.

Braun (1900) defined the characters of the Phyllobothriidæ thus:—"Head unarmed, with four sessile or pedunculated

bothridia which are either simple, complicated, or divided up into areolæ, or furnished with accessory suckers. Neck present or absent. Genital pores marginal, regularly or irregularly alternating. Eggs often spindle-shaped. Segments frequently separate from the chain before maturity."

Van Beneden (1850) erected three new genera in this family, with the following characters :—

(1) *Echeneibothrium.*—The four bothridia of the scolex are borne on long, protractile pedicels. They are extraordinarily variable in form, and are distinguished by the regular folds which develop along the whole length of these organs and which make them resemble the suckers on the head of fish of the genus *Echeneis.*

Type-species :—*Echeneibothrium minimum* van Beneden, 1850.

(2) *Phyllobothrium.*—The four bothridia are sessile and carved out of the head ; they are extremely mobile, and are curled like the leaf of a lettuce.

Type-species :—*Phyllobothrium lactuca* van Beneden, 1850.

(3) *Anthobothrium.*—The four bothridia are hollow in the middle and have the shape of a vase or a monopetalous flower, or they may extend like a rounded disc borne on a long, protractile pedicel. The margins are not curled like a leaf, and parallel folds are not formed.

Type-species :—*Anthobothrium cornucopia* van Beneden, 1850.

At that time, when only two species of each of the above genera were known, the distinction between them was well defined. Thus the genus *Echeneibothrium* included those forms in which the entire surface of the bothridium was split up into loculi by the development of transverse or longitudinal septa. The genus *Phyllobothrium* was distinguished by the fact that the bothridia were sessile and curled or folded like a lettuce leaf, whilst in the genus *Anthobothrium* they assumed the form of a horn or vase.

Since then a large number of species belonging to this family have been described, and these show a very wide range of variation in the form of their bothridia, intermediate in character between the generic types defined by van Beneden. It has been the experience of all helminthologists who have devoted time to the study of these forms that it is impossible in most cases to decide to which of the latter two genera a particular species belongs, except in the case of *Phyllobothrium lactuca*, which is characterized by being much more gross and fleshy than other species of this group. Not only is this so, but species are known in which the margins of the bothridia are provided with a continuous series of loculi which, when the bothridium is unduly extended, may easily be mistaken for that of a species of *Echeneibothrium.* Linton (1889)

included such species in a new genus to which he gave the name *Crossobothrium*.

Beauchamp (1905) points out that, owing to the absence of hooks in this family, and to the variable form of the bothridia, great confusion exists in the nomenclature, especially with reference to the characters of the genera as defined by the different authors, each author "interpreting the generic characters after his own fashion and fitting different species into them." Beauchamp did not define the family, but he distinguished two types or tribes which comprise the entire family, viz. :—

(1) Phyllobothriens, the characters of which he did not describe ; the type-genus is *Phyllobothrium* van Ben., 1850, characterized by having the surface of the bothridia plain and not split up into areolæ, although the margins may be crenulate or differentiated in a variety of ways. He defined the genus thus :—

"*Phyllobothrium.*—Bothridia circular or oval ; often folded, surface smooth, except sometimes at the edge ; often with an accessory sucker ; myzorhynchus absent or rudimentary."

(2) Echeneibothriens, the characters of which he did not give. Type-genus *Echeneibothrium* van Ben., 1850, characterized by having the surface of the bothridia split up into a varying number of areolæ. He defined the genus thus :—

"*Echeneibothrium.*—Bothridia elongated ; subdivided by muscular ridges into oblong areolæ ; no accessory suckers ; myzorhynchus sometimes well developed."

Beauchamp pointed out that the characters on which the numerous genera of the Phyllobothriens were founded had reference to (1) whether the bothridia were stalked or sessile, (2) whether accessory suckers were present or absent, (3) the form of the bothridia, (4) the presence or absence of a myzorhynchus ; and he stated that such characters are not distinctive and are of no value because, as the bothridia are extremely muscular and mobile, it was possible for the same species to assume, both in life and when preserved, all the different appearances intermediate between the *Phyllobothrium* and the *Anthobothrium* type.

Linton (1924) writes :—

"In common with others who have attempted to classify Selachian Cestodes, I have experienced much difficulty with those genera of the Phyllobothriidæ which are characterized by having a scolex with four unarmed bothria, each provided with an auxiliary sucker at its anterior end, and without costæ.

"The generic names which I have used for members of this group are : *Anthocephalum* Linton, *Calyptrobothrium* Monticelli, *Crossobothrium* Linton, *Monorygma* Diesing, *Orygmatobothrium* Diesing, and *Phyllobothrium* Beneden.

"*As I have interpreted these genera, they may be arranged according to the following scheme*:—

1. Auxiliary acetabula relatively small, borders of bothria usually thin and flexible, often folded or crumpled	2.
Auxiliary acetabula more or less cup-shaped ..	3.
2. Bothria in pairs, leaf-like with crenulate borders	*Phyllobothrium.*
Bothria cruciform with crenulated borders....	*Anthocephalum.*
Bothria cruciform, borders not crenulate......	*Crossobothrium.*
3. Bothria with sphincter muscle on border	*Orygmatobothrium.*
Bothria plain, acetabula cup-shaped	*Monorygma.*
Acetabula large, horseshoe-shaped	*Calyptrobothrium.*

"Consideration is not here given to two characters which are usually mentioned in descriptions of these genera, that is, the presence or absence of a myzorhynchus and the pedicelled or sessile condition of the bothria.

"As to these features, it may be said that whether the bothria are pedicelled or not is often very difficult to determine in these strongly contractile forms, unless one has seen them when they were actively mobile. Furthermore, the presence or absence of a myzorhynchus, unless it is represented by a permanent sucker as in *Echeneibothrium*, is of little importance, since it is an evanescent structure found in a variety of larval forms, as, for instance, *Scolex polymorphus*, and may be retained, more or less discernibly, in scoleces which have developed strobiles.

"It is significant that Zschokke, in his admirable Monograph, gives evidence of the unsettled state of the systematic relations of such forms as are here being considered, as, for example, *Orygmatobothrium* (*Phyllobothrium*) *dohrnii* Oerley and *Anthobothrium* (*Orygmatobothrium*) *musteli* van Beneden; other examples could be cited.

"The material which I have does not warrant an attempt at the revision of these difficult forms. The foregoing observations are made in the hope that they may prove of assistance to future workers."

The similarity of the genitalia of the various species of this family is so great that it appears impossible to utilise these organs as a basis of classification except for the differentiation of species, and the same is true with regard to the vitelline glands and the musculature. The characters of the head, therefore, at present assume considerable importance for purposes of classification.

The writer in 1925 retained van Beneden's three genera, and stated that the genera *Phyllobothrium* and *Anthobothrium* were to be distinguished by the fact that in the former each bothridium bore an accessory sucker which was absent in the latter. He pointed out at the time, however, that, owing to

the folding of the bothridia, these suckers are often very difficult to locate, and he is now satisfied that as a differential generic character such a small point is both inadequate and unsatisfactory. They are accordingly united, and only two of van Beneden's genera, viz., *Echeneibothrium* and *Phyllobothrium*, are recognized.

Characters of the Family Phyllobothriidæ *Braun*, 1900.

Synonyms :—Tribe Phyllobothriens van Ben., 1850.
Subfamily Phyllobothridea Carus, 1863.
Subfamily Phyllobothria Leuckart, 1886.

Head unarmed, with four pedunculated or sessile bothridia, which are simple, complicated, or divided up into areolæ, or furnished with accessory suckers. Neck present or absent. Genital pores marginal, unilateral, or regularly or irregularly alternate ; eggs often spindle-shaped ; segments frequently separate from the chain before maturity. Type-genus :—*Phyllobothrium* van Ben., 1850.

Key to Genera.

1. Bothridia globular or cylindrical, hollow and open at both ends	PITHOPHORUS, p. 231.
Bothridium not a hollow cylindrical globe or bag	2.
2. Myzorhynchus armed with suckers ..	MYZOPHYLLOBOTHRIUM, [p. 225.
Myzorhynchus, even when present, not armed with suckers	3.
3. Entire face of bothridium divided into loculi	ECHENEIBOTHRIUM, p. 209.
Entire face of bothridium not divided up into loculi	4.
4. Bothridia simple or complicated, with or without minute loculi round their margins. Accessory suckers present or absent	PHYLLOBOTHRIUM, p. 179.
Proximal portion of each bothridium cylindrical, bearing two semicircular flaps at its distal extremity, margins with small loculi. Accessory suckers absent	CARPOBOTHRIUM, p. 229.

Genus I. PHYLLOBOTHRIUM van Beneden, 1850.

Synonymy extensive, including the following :—*Anthobothrium* van Ben., 1850 ; *Crossobothrium* Linton, 1889 ; *Anthocephalum* Linton, 1890 ; *Rhinebothrium (ceylonicum)* Shipley & Hornell, 1906.

The original description of this genus was as follows :—"The four bothridia are sessile, cut out on the external face of the head and enjoying very great mobility ; they are curled and folded like the leaves of a lettuce." Type-species :—*Phyllo bothrium lactuca* van Ben., 1850, from *Mustelus vulgaris*.

According to Braun (1900) the characters of the genus are as follows :—" Bothridia sessile, large, with free margins strongly folded. Sometimes with anterior accessory suckers. Neck long."

Linton described the genus thus :—" Body articulate, tæniæform, head separated from the body by a neck, with four opposite sessile bothridia, each bothrium lacinio-crispate on the margin, and provided with a single ampulla-like supplmental disc. Genital apertures marginal."

The characters of the genus are emended as follows :— Body segmented. The head bears four bothridia, which in one (or two ?) species are large and fleshy ; they may be sessile or pedunculated, and their surfaces may be simple or curled and folded ; their margins may be entire, frilled, and crenulate or they may bear minute sucker-like organs. Accessory suckers sometimes present. and situated either anteriorly, or laterally, or near the centre of the bothridium ; in species with fleshy bothridia they are sometimes difficult to locate. Neck present or absent ; genital pores marginal. Parasitic in elasmobranch fishes, reptiles and mammals. Type-species :— *Phyllobothrium lactuca* van Ben., 1850.

Key to Species of Phyllobothrium.

1. Each bothridium divided into two	2.
Each bothridium not divided into two	3.
2. Each bothridium hinged in the middle ..	*P. lintoni*, p. 197.
Bothridia not hinged in the middle	*P. dagnalli*, p. 200.
3. Each bothridium with a marginal row of loculi	*P. variabile*, p. 187.
Bothridia without marginal loculi........	4.
4. Myzorhynchus prominent, bothridia thin, leaf-like	*P. tumidum*, p. 199.
Myzorhynchus absent	5.
5. Pores unilateral	6.
Pores irregularly alternate	7.
6. Large worms; bothridia shallow, cup-like ; accessory suckers absent	8.
Small worms; bothridia with large accessory suckers	*P. minutum*, p. 194.
7. Head globular, fleshy, up to 6 mm. in breadth ; separate bothridia and accessory suckers difficult to identify........	*P. lactuca*, p. 181.
Head not globular or fleshy	9.
8. Worms 15 to 30 cm. in length	*P. giganteum*, p. 186.
Worms about 1 cm. in length	*P. floraforme*, p. 198.
9. Bothridia flat, membranous, ill defined ; with ragged margins ; without accessory suckers	*P. panjadi*, p. 195.
Four bothridia well defined, each with an accessory sucker	*P. foliatum*, p. 190.
Four bothridia well defined, without accessory sucker ; minute worms 3 mm. in length	***P. microsomum*, p. 205.**

(1) **Phyllobothrium lactuca** van Ben., 1850. (Figs. 66, 67, & 68.)

Synonyms:—*Rhinebothrium ceylonicum* Shipley & Hornell, 1906.
Phyllobothrium compactum Southwell & Prashad, 1920.

From *Dasybatus kuhli*, *D. walga*, and *Galeocerdo arcticus*, Pearl Banks, Ceylon. Southwell.

The worms measure up to 6 or 7 cm. in length and have a breadth of about 4 mm.; they are composed of numerous segments, most of which are broader than long; the last ones frequently assume a length of 5 mm. or more; the genital apertures are marginal and irregularly alternate; their

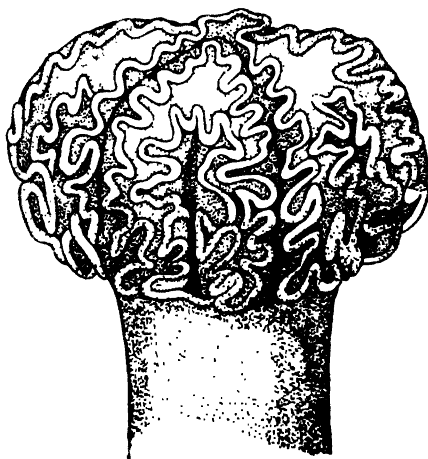


Fig. 66.—*Phyllobothrium lactuca*. Head, magnification unknown. (After van Beneden.)

position varies according to the state of contraction of the segments; they may lie anteriorly to the middle or posteriorly to the middle.

Head. The head is massive, almost globular, and has a diameter of about 6 mm. or more; it consists of four very large sessile bothridia whose margins are curled and folded like the leaves of a lettuce. In his original figure van Beneden did not show accessory suckers, but in a later paper (1858) he stated that the margin of each bothridium bore an accessory sucker, which he figured. Accessory suckers were seen on the bothridia in the specimens described below, except in two or three cases.

The muscular system is strongly developed and consists of stout bundles (which are not subcuticular), internally to

which lies a well-defined layer of circular fibres, dividing the parenchyma into cortex and medulla (fig. 67). In fact, the musculature resembles that of a worm like *Tænia crassicollis*.

Testes. The testes consist of numerous rounded structures occurring from near the anterior portion of the proglottid to

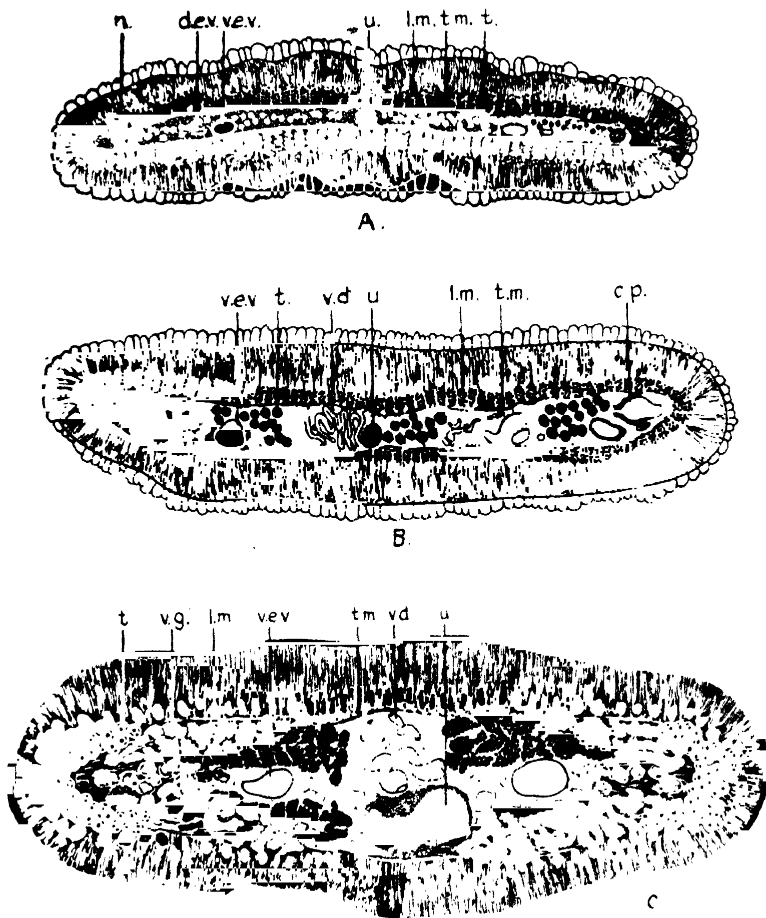


Fig. 67.—*Phyllobothrium lactuca.* Transverse sections of: A, immature, B, mature, and C, nearly gravid segments, showing gradual disappearance of longitudinal musculature; × 34. (Orig.)

behind the genital opening. They occupy the central field, and are situated at a much deeper level than the vitelline glands which lie external to them. Each testis is about 50 μ in diameter, and is much smaller than shown by van Beneden;

moreover, the number of testes in each proglottid is much larger than indicated in his figure.

Vas deferens. From each of the testes arises a fine tubule, and the ducts from the various testes unite together to form a single median vas deferens. This is a very much coiled, elongated, tubular structure which continues to the cirrus sac; the terminal portion forms the ejaculatory duct, and the outer end of the tube is continuous with the outer extremity of the cirrus sac. At the time of protrusion the ejaculatory duct is a double tube, the outer one being the everted part of the cirrus sac, while the inner is the terminal portion of the vas deferens. This evertible portion—the penis or the cirrus—is unarmed.

Ovary. The ovary consists of two large lobes lying one on each side of the centre line, near the posterior end of the segment; they are connected with each other by a median isthmus. Each of the lateral halves is double, as has been described by Haswell for *P. vagans.* The margins of the ovary is very much crenated.

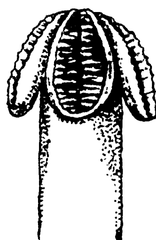


Fig. 68.—*Phyllobothrium lactuca.* Head, × 5. (After Shipley and Hornell.)

Oviduct. The oviduct begins ventrally to the ovarian isthmus in a pouch-like structure which is known as the "swallowing apparatus." From the swallowing apparatus the oviduct runs backwards ventrally to the shell gland and the receptaculum seminis and then curves upwards to the dorsal surface; it then continues forwards dorsally to the vagina and the isthmus of the ovary where it ends blindly. In its course it receives, just before curving upwards, the fertilizing duct from the receptaculum seminis. The vitelline duct opens into it a little anteriorly. The distal portion of the oviduct (which has been designated the oötype, or primary uterus) joins the secondary uterus by a longitudinal slit on the ventral surface of the latter organ.

Vagina. The vagina opens immediately in front of the male pore by a fairly broad aperture into the shallow genital pit, which is situated nearer the posterior than the anterior

extremity. Its terminal portion is swollen to form a barrel-shaped structure which probably serves for the storage of spermatozoa until they can find their way to the bag-like receptaculum seminis at the end of the sinuous vaginal duct. From the barrel-shaped dilatation a thin tube leads backwards and upwards. A little above the origin of the main vas deferens this tube curves backwards and is continued dorsally to the secondary uterus; eventually, below the isthmus of the ovary, it is dilated to form the vesicula seminalis. From the bag-like receptaculum seminis the fertilizing duct leads to the oviduct, as has already been described.

Vitelline Glands. The vitelline glands are situated laterally and externally to the longitudinal muscles. They are ovoid structures 400 μ in diameter. A fine duct leads from each glandular unit; these tubules then unite into two ducts, one on either side, and the pair further unite to form a median duct which opens into the oviduct a little below the shell gland.

Shell Gland. The shell gland is a compact structure surrounding that portion of the oviduct which is situated a little in front of the opening of the vitelline duct into the oviduct. As seen in sections, the shell gland appears to be connected with the oviduct by minute tubules, through which the secretion flows.

Uterus. The uterus is a large elliptical chamber extending from close to the isthmus of the ovary to very near the anterior end of the proglottid. It has no external aperture, and the dehiscence of the proglottid probably takes place in the same manner as has been described by Haswell for *P. vagans*; in segments still attached it is, however, only a tubular structure without any eggs, and only develops fully after leaving the chain.

Rhinebothrium ceylonicum Shipley & Hornell, 1906.

"Although the stalks or pedicels of the bothridia (if, indeed, they exist at all) must be very short, the specimens about to be described seem to us to belong to Linton's genus *Rhinebothrium*. The head bears four fleshy bothridia at the four angles, back to back. Each bothridium is divided into two halves, as in *Rh. flexile* Linton, by a longitudinal groove, and each half bears a number of horizontal slit-like areolas placed transversely. The number of these areolas was not exactly made out, but is somewhere about twenty. The whole recalls a rasp, after which the creature takes its name. In the preserved specimens, of which only two were taken, the head was rather broader than it was long, its greatest breadth being 4 mm. Judging from the figure taken of the head whilst alive, the length about equalled the breadth. In the living form also the bothridia seem more clearly distinct from one another and from the head; in the preserved form they have all shrunk together.

"The length of the body of our longer preserved specimens is 5 cm., but, as in both, the tail is curved up in the lateral plane, and perhaps, if uncoiled, the length would be 5·8 or 6 cm. When alive, it measured 9 inches. The body is stout and wide. Our second specimen—also giving off mature proglottids—was a little more than half this size. In the middle, which is the widest portion, it is 3 mm. broad, and it tapers away slightly both in front and behind. It is 2 mm. thick and is very stiff and firm in the preserved condition.

"The neck is short, and the proglottides are at first very narrow from front to back. There seems to be a curious false strobilization whereby five or six segments are grouped together, but this may be an individual character. The posterior angle ot each proglottis was salient, and projected slightly over the succeeding proglottis. Only at the hinder end are the proglottides as long as they are broad, and only the last three or four are longer than they are broad. The incurved tail seemed characteristic, at any rate it occurred in both our specimens. The body was too thick and too opaque for us to make out any details of the internal anatomy." (*Shipley & Hornell.*)

The author obtained a total of eleven specimens of this parasite on three occasions from the intestines of *Dasybatus kuhli*, and once from the intestine of *D. walga*. They were examined immediately after preservation and provisionally referred to the above species. As a result of a careful re-examination of these specimens it is now clear that although each bothridium appeared to be divided into two halves by a longitudinal groove, each half bearing a number of horizontal slit-like areolæ placed transversely, this appearance is quite misleading ; it is caused by the folding and frilling of the somewhat thickened margin of the bothridium in precisely the manner shown by van Beneden in *Phyllobothrium lactuca.* The appearance of the head is subject to considerable variation, but the author is satisfied that the specimens referred by Shipley and Hornell to *Rhinebothrium ceylonicum*, and also the eleven worms provisionally referred to the same species by the present author, are undoubtedly examples of *P. lactuca* van Ben. The anatomy of these latter agrees in detail with that of *P. lactuca.*

Phyllobothrium compactum Southwell & Prashad, 1920.

The head has a very compact appearance owing to the sessile nature of the large, fleshy, and well-developed bothridia. The edges of the bothridia are slightly crumpled and no accessory suckers could be seen. The writer is now of opinion that, although an accessory sucker could not be seen, this species is identical with *P. lactuca.*

(2) **Phyllobothrium giganteum** (van Ben., 1858). (Fig. 69.)

Synonyms :—*Anthobothrium giganteum* van Ben., 1858.
" *Anthobothrium rugosum* Shipley & Hornell, 1906.

From *Dasybatus walga*, Pearl Banks, Ceylon. Hornell.

"This species is characterized by the peculiar shape of the bothridia, each bothridium having a transverse orifice like

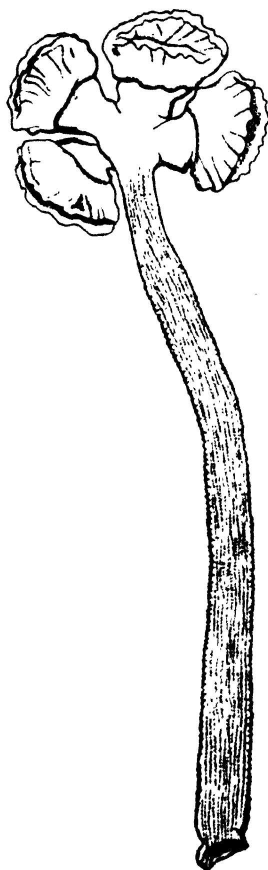


Fig. 69.—*Phyllobothrium giganteum*. Head and neck, × 5. (After Shipley and Hornell.)

that of a plagiostome fish. The bothridia are quite round, and look like the suckers of a pedunculated tænia. The neck is fairly long. Segments appear slowly, and in the adults they are a little longer than broad; when detached they are concave

posteriorly. Genital pores unilateral ; the cirrus is very long and without rugosities. Parenchyma fills up the middle of the segment ; the eggs are shaped like a spindle. Length of worm 15 cm ; posterior width 2 to 3 mm. ; bothridia 1 mm. Found in the intestine of *Galeus canis*. This species differs from *A. cornucopia* in the absence of lobules ; it is distinguished from *A. musteli* by its shape which is more robust, and by its bothridia which are always rounded. Its shape resembles that of *A. perfectum*, but the bothridia of this last species are always boat-shaped with a sucker at the apex, and the eggs in *A. perfectum*, although they are somewhat elongated, are not spindle-shaped." (*van Beneden.*)

Anthobothrium rugosum Shipley & Hornell, 1906.

Worms up to 30 cm. in length with four bothridia, each borne on a short stout stalk. Each bothridium consists of a bag-like sucker having puckered margins ; the head looks like a pressed flower. Neck about 6 mm. in length. The authors pointed out that "the species is distinguished from *A. cornucopia* and *A. musteli* van Ben. by the wrinkling of the bothridium and the shape of the body, and from *A. elegantissimum* Lönn., by the absence of a myzorhynchus. . . . Its most striking characteristics are the crumpled suckers, the stout neck and the longitudinal muscles." The writer considers it identical with *A. giganteum* van Ben.

(3) **Phyllobothrium variabile** (Linton, 1889). (Figs. 70, 71, & 72.)

Synonyms :—*Spongiobothrium variabile* Linton, 1889.
Echeneibothrium simplex Shipley & Hornell, 1906.

From *Dasybatus kuhli* and *D. walga*, Pearl Banks, Ceylon. Hornell ; Southwell.

Linton (1889) described the genus *Spongiobothrium* as follows :—"Body articulate, tæniæform. Head separated from body by neck. Bothria four in lateral pairs, pedicelled, with crisp-folded or auriculate edges which are crenulate, and the auriculate flaps finely costate on account of a marginal row of loculi with muscular borders ; unarmed and without transverse costæ on face. No myzorhynchus, no supplemental discs. Genital apertures marginal." He states that "the genus combines many of the characters of *Echeneibothrium* and *Phyllobothrium*. It differs from the former in the laciniæ of the bothria and in the absence of a terminal haustellum ; from the latter in having pedicelled instead of sessile bothria, and in the transverse costæ on the bothria. . . . The crisp-folded edges of the bothria produce an effect which suggests

Leuckart's *Bothriocephalus* (= *Anthobothrium auriculatum* var. *centrifolium* Dies.). The costate flaps suggest relationship to *Rhinebothrium*."

Linton's specimens of *A. variabile* ranged in length from 2·1 to 9 cm.; a short neck was present. The four bothridia were pedicelled, fan-shaped, in lateral pairs, their faces and margins having numerous frill-like lobes which are sometimes gathered into a more or less compact mass of crisp folds, sometimes expanded into long, curved, auriculate or leaf-like flaps. The borders of the bothridia bear a row of small loculi which give a crenulate effect to the margins and a costate appearance to the auriculate flaps. Genital pores in a marginal depression in the posterior third of the segment. Linton stated that the ovary consisted of two sets of radiating tubes situated in the posterior end of the segment, the testes being crowded into the anterior half. The centre of the segment is occupied by the convoluted vas deferens; the cirrus is densely



Fig. 70.—*Phyllobothrium variabile.* Heads, × 10. (After Linton.)

covered with spines. There is a large vaginal sinus measuring 200 μ in length. Linton also mentioned the presence, in free proglottides, of a large oval aperture (for the escape of ova) in the lateral face of the segment, which measured 400 by 300 μ. The living ova measured 180 μ in diameter, and each consisted of a transparent globular pellicle within which were from three to five granular masses which seemed to be nuclei undergoing normal development; each granular mass had a diameter of 20 μ.

Specimens of this parasite have been obtained from the intestines of *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

The characteristic feature of this species is the presence of an enormous genital pore and atrium, situated laterally in the posterior quarter of the segment. As a result, the cirrus pouch is in close proximity with the apex of the poral ovarian lobe.

Testes. These vary in number from about thirty-four to forty, and are situated in the median field in front of the ovary;

when fully developed they have a diameter of about 40 μ; they persist to the last segment.

Vas deferens. The cirrus pouch is small, lies posteriorly to the vagina, and immediately in front of the aporal lobe of the ovary, which it practically touches; in no case was the cirrus everted, and it was impossible to decide whether it was armed or not. The vas deferens on leaving the pouch turns anteriorly and forms a dense median coil near the antero-posterior extremity. Seminal vesicle absent.

Ovary. This is a bilobed or U-shaped organ situated pos-

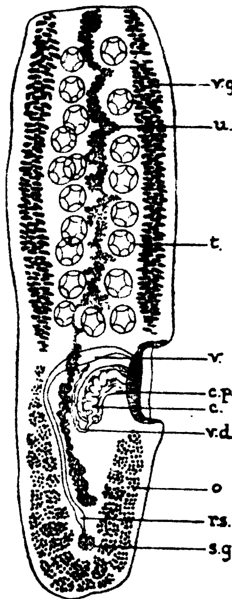


Fig. 71.—*Phyllobothrium variabile.* Mature segment, × 75. (After Southwell.)

teriorly and composed of large, irregularly shaped acini. As noted above, its poral limb extends to the cirrus pouch.

Vagina. From the pore the vagina runs in front of the cirrus pouch as a slightly dilated tube. At the extremity of the pouch it turns and runs to the ovary, dilating near the latter organ into a small receptaculum seminis. On account of the pore being situated posteriorly the whole vagina is very short; shell gland apparently absent.

Vitelline Glands. These lie along each lateral margin and consist of a dense mass of elongated acini, having their long axes transversely to the length of the segment.

Uterus. At first this consists of a simple tube running anteriorly in the mid-antero-posterior axis; its posterior extremity is in communication with the oviduct; later on it becomes coiled and dilated, and extends to the extreme anterior margin of the segment. Proglottides containing a well-developed uterus have not been obtained.

The form of the bothridia and the presence of a large genital atrium in the posterior part of the segment leave no room for doubt that these specimens are identical with *Spongiobothrium variabile* Linton, 1889.

Echeneibothrium simplex (Shipley & Hornell, 1906).

Strobila 2 cm. in length and consisting of about 100 segments. The head carries four stalked bothridia, each shaped like

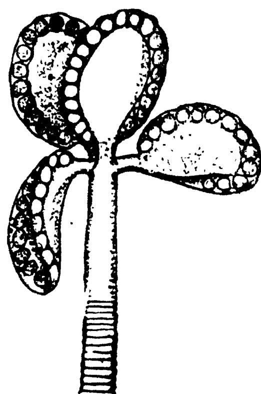


Fig. 72.—*Phyllobothrium variabile.* Head, × 35. (After Shipley and Hornell.)

a violet-leaf; the edge of each is divided by horizontal ridges into about twenty-two areolæ; there is no myzorhynchus or neck; genital pores lateral and irregularly alternate. Only the last 6 or 7 segments are longer than broad. It seems extremely probable that Shipley and Hornell's species is identical with that described by Linton.

(4) **Phyllobothrium foliatum** Linton, 1890. (Figs. 73, 74, 75, & 76.)

From *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Southwell.

The largest worm measures 12·5 cm. in length and the maximum breadth is [illegible]·4 mm., and is composed of a large number of segments (over 400); the last one (mature, but not gravid) measures about 1·8 mm. in length and 1·3 mm. in breadth. The genital pores are irregularly alternate and are situated slightly in front of the middle of the lateral margins of the segments.

The neck is about 7 mm. in length.

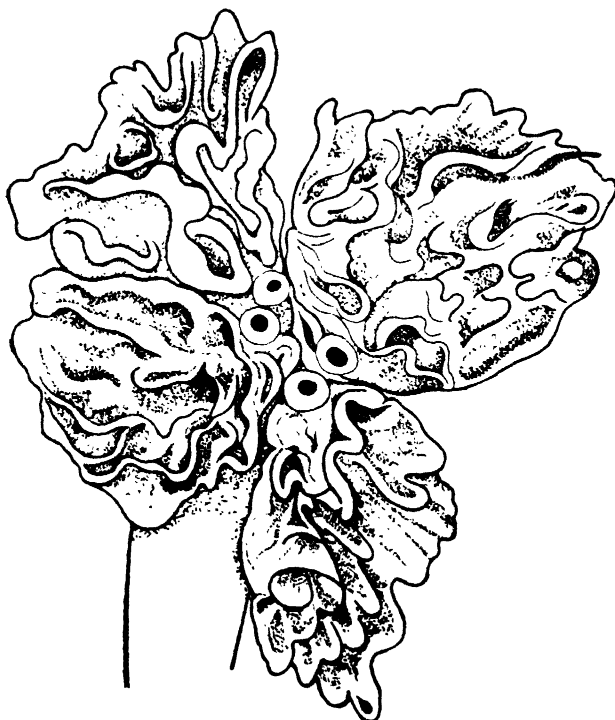


Fig. 73.—*Phyllobothrium foliatum.* Head, viewed *en face*, × about 20. (After Southwell.)

Head. The head bears four flattened bothridia which assume a variety of forms. Usually they are quite flat, and have the shape of a quadrant of a circle. They are thin and leaf-like and have one face quite smooth. The other face bears a number of ray-like projections figured by Southwell and Prashad in 1920. Each bothridium bears a prominent accessory sucker having a diameter of 250 μ and situated just where it joins on to the neck.

They have a maximum length of about 2 mm. and a maximum breadth of about 1·5 mm. The largest head had a length of 4 and a breadth of 4 mm.

Nervous System. In transverse sections a single large nerve can be seen running longitudinally externally to the two small excretory vessels. It is not known whether the genital ducts pass dorsally or ventrally to the nerve.

Excretory System. There are two small vessels of about equal size in young segments running along each lateral margin. In mature segments the ventral vessel is much larger than the dorsal vessel. The genital ducts pass between them.

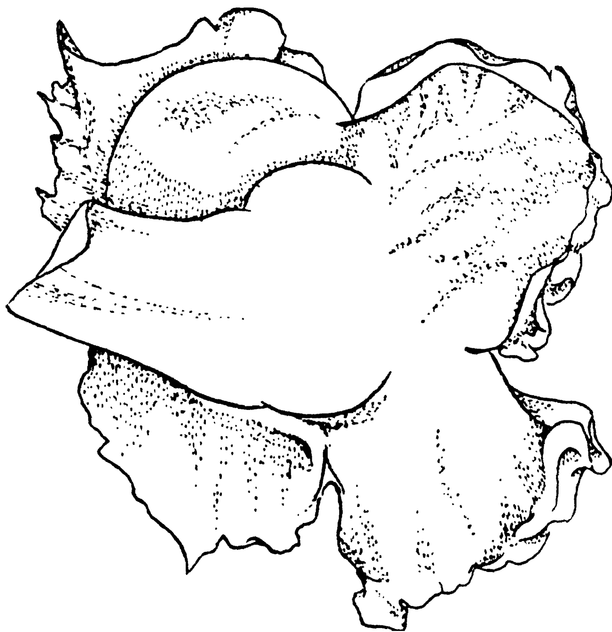


Fig. 74.—*Phyllobothrium foliatum.* View of back of head, × about 20. (After Southwell.)

Muscular System. Immediately below the cuticle there is a number of well-developed bundles of dorso-ventral fasciæ. Internally to these are the numerous small, closely packed bundles of longitudinal fibres. Circular muscles are poorly developed.

Testes and Vas deferens. The testes are numerous and occupy the central field extending on both sides posteriorly to the cirrus pouch. The latter is very large and prominent, and opens into a marked genital sinus which is covered with

relatively large spinules. Within the cirrus pouch the vas deferens is very long indeed, and forms a series of close

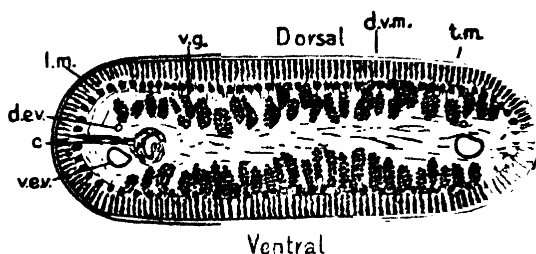


Fig. 75.—*Phyllobothrium foliatum.* Transverse section of almost mature segment, × 50. (After Southwell.)

coils. It appears to be covered with cilia throughout its length. The cirrus is armed with spinules and has an enlarged

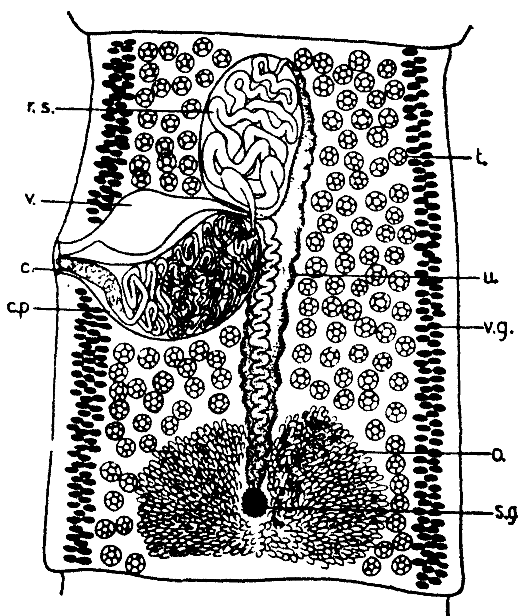


Fig. 76.—*Phyllobothrium foliatum.* Mature segment. × 52. (After Southwell.)

extremity. Immediately on leaving the cirrus pouch, in the median direction, the vas deferens becomes thickened

and thrown into a series of coils which are enclosed in a prominent sac, the external seminal vesicle, situated anteriorly in the longitudinal axis.

Ovary and Oviduct. The ovary is bilobed, prominent, and situated posteriorly. The oviduct runs in the median longitudinal axis as a very long and coiled spiral tube; it passes anteriorly to the cirrus pouch and dilates into a large vesicle immediately before opening into the genital sinus. No receptaculum seminis was seen; if present it is very small. There is a large shell gland situated between the lobes of the ovary.

Vitelline Glands. These cover almost the whole of the dorsal and ventral surfaces, but they are most condensed laterally. A rudimentary uterus extends as a small elongated sac in the longitudinal axis.

(5) **Phyllobothrium minutum** Shipley & Hornell, 1906. (Fig. 77.)

From *Carcharias melanopterus*, Pearl Banks, Ceylon. Hornell.

The worm measures about 8 mm. in length, 300 μ in breadth, and contains from 80 to 100 proglottides. The neck is long

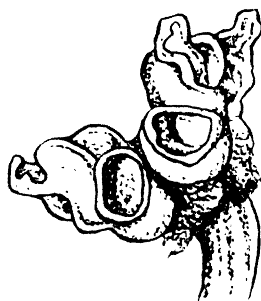


Fig. 77.—*Phyllobothrium minutum.* Head, ×80. (After Shipley and Hornell.)

and hair-like. The head is small and bears four bothridia each with a large accessory sucker or areola situated near the centre. The edges of the bothridia are crumpled, at least slightly so. The anterior proglottides are a little broader than long, but the posterior ones are at least one and a half times longer than broad. The reproductive pores are unilateral.

This species is distinguished by the presence of a large accessory sucker near the centre of each bothridium. (After Shipley and Hornell.)

(6) **Phyllobothrium panjadi** (Shipley & Hornell, 1909). (Fig. 78.)

Synonym :—*Anthobothrium crispum* Shipley & Hornell, 1906.

From (1) *Ætomylæus maculatus* and (2) *Stoasodon narinari*, Pearl Banks, Ceylon. Hornell ; Southwell.

"A few specimens of this species were taken from the intestine of *Myliobatis maculata*. For elasmobranch cestodes

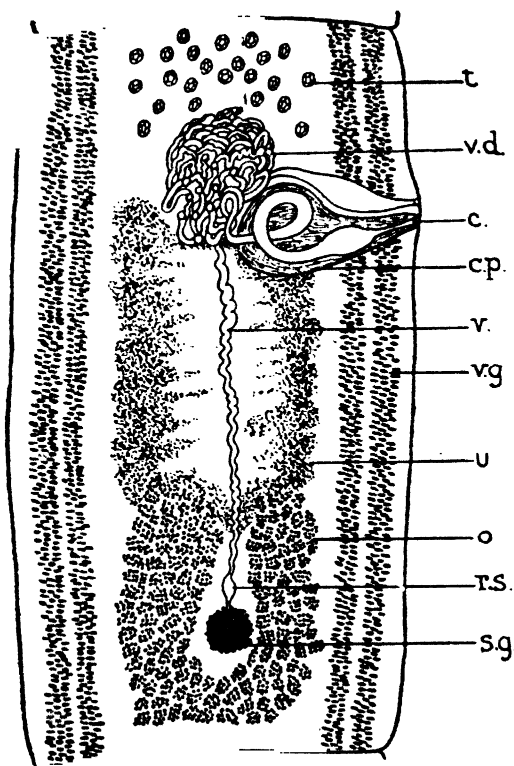


Fig. 78.—*Phyllobothrium panjadi*. Mature segment, × 69. (After Southwell.)

they are large tapeworms, reaching a length of 8 or 9 cm. The head is 3·5 mm. in diameter. It is produced into bothridia whose edges are much crumpled, frilled, fringed, and subdivided. In some cases the subdivision extends a good way towards the pedicel, and gives the head the appearance of consisting of six or eight bothridia. The pedicels are very short and the bothridia seem to be almost sessile. No myzorhynchus was visible.

"The neck is very long, and even quite posteriorly the proglottides show very little demarcation. There is no indentation of any sort. The line which separates one proglottis from its neighbour is usually clear and sharp in the centre, but it hardly reaches the sides of the tapeworm. These latter are quite smooth, and, except that the body slightly increases in thickness, they would be quite parallel. The neck is about 700 μ in width, the posterior part of the body 1 mm. in width.

"The specimens did not stain well, and all that could be made out was an L-shaped structure, of which one arm represents the reproductive ducts running to the pore and the other arm the uterus. The reproductive pores are irregularly alternate. This form is much more slender than the *A. rugosum* of *Trygon walga*, and the bothridia are less stalked." (*Shipley & Hornell.*)

The genital pores are marginal, irregularly alternate, and are situated in the anterior third of the segment. The margins of the segments are straight; the last segment measures 1·4 mm. in length and 800 μ in breadth. The neck is very long. Details of the muscular, excretory, and nervous systems are not known, but in segments mounted whole the longitudinal fibres are very prominent.

Testes. In immature segments the testes are crowded together in two antero-posterior areas, one on each side of the median axis; they spread out a little when mature. The number of testes is about 100; when fully developed they each have a diameter of about 36 μ.

Vas deferens. The cirrus pouch lies posteriorly to the vagina and is pyriform in shape, extending to the middle of the segment. The cirrus is also pyriform in shape, with the pointed extremity lateral; it is unarmed. Behind the cirrus the vas deferens is wide and forms a few coils inside the pouch. Outside the pouch it turns anteriorly and forms a number of dense coils almost in the median antero-posterior axis. No seminal vesicle was observed.

Ovary. This is a massive bilobed organ situated posteriorly and made up of rounded acini.

Vagina. From the pore the vagina runs anterior to the cirrus pouch and is dilated; at the median extremity of the latter organ it narrows and turns sharply posterior, running in the antero-posterior axis as a coiled tube. Near the shell gland it dilates into a small receptaculum seminis.

Shell Gland. This is a conspicuous organ, measuring about 70 μ, situated between the two lobes of the ovary.

Vitelline Glands. These consist of a dense mass of acini lying along each lateral margin. The acini are almost linear

in outline and closely crowded together ; they lie both external and median to the water vessel.

Uterus. The rudiment of the uterus is very prominent even before the testes are fully developed. In mature segments it is a saccular organ extending anteriorly just beyond the cirrus pouch. Apparently the oviduct opens into the uterus posteriorly. No ripe segments were seen.

The form of the bothridia, the long neck, and the anteriorly placed genital pore leave little room for doubt that the specimen described above is identical with *A. panjadi* (Shipley & Hornell), 1909 (=*A. crispum*, Shipley & Hornell, 1906).

As the name *crispum* was occupied for a species created by Molin in 1858, Shipley changed it to *panjadi* in 1909. The species resembles *P. tumidum* Linton, except that it bears no accessory suckers.

(7) **Phyllobothrium lintoni** (Southwell, 1912). (Fig. 79.)

Synonym :—*Spongiobothrium lintoni* Southwell, 1912.

From (1) *Rhynchobatus djiddensis* and (2) *Urogymnus asperrimus*, Pearl Banks, Ceylon. Southwell.

"The head consists of four bothridia with a row of tiny loculi round the edges. Each bothridium is roughly oval in shape, and is suspended by a rather short stalk. Opposite the point of attachment each appears to be almost divided transversely into two halves and their edges are indented. Placed centrally and opposite to the point of attachment is a minute flask-shaped depression on the face of each bothridium, which at first was mistaken for a sucker. Careful examination, however, showed that the two halves of a bothridium are capable of movement, simulating the movements of the parts of a hinge. When the two faces of the two parts of the bothridium are opposed, the central depression is noticeable, but when they are separated from each other and flattened, this structure is hardly visible under a low power. In shape the bothridia resemble those of *Rhinebothrium insignia* Southwell, but the areolæ are very differently distributed. The number of loculi round the margin varies greatly ; in some specimens they are very pronounced, whilst in others they are only found with difficulty. There are no transverse or longitudinal septa and no myzorhynchus. The average breadth of the head is 1 mm. and the length 600 μ. The neck is very short, being about 400 μ long and about 200 μ broad ; the anterior half is usually clear and transparent. The length of the worm is 2 cm. The average number of proglottides is twelve. The first segment is square, or nearly so ; they rapidly elongate, however. The sixth segment is twice as long as broad, and the last one is 4 mm. long and

500 μ broad. The sides of the proglottides are slightly convex. The genital apertures are lateral and irregularly alternate. Only the last two segments appear to be mature. The penis is 600 μ long, very narrow, with a bulbous base." (*Southwell.*)

This species differs from *P. variabile* (Linton) in (1) being smaller, (2) having fewer segments, and (3) having each bothridium divided into two halves.

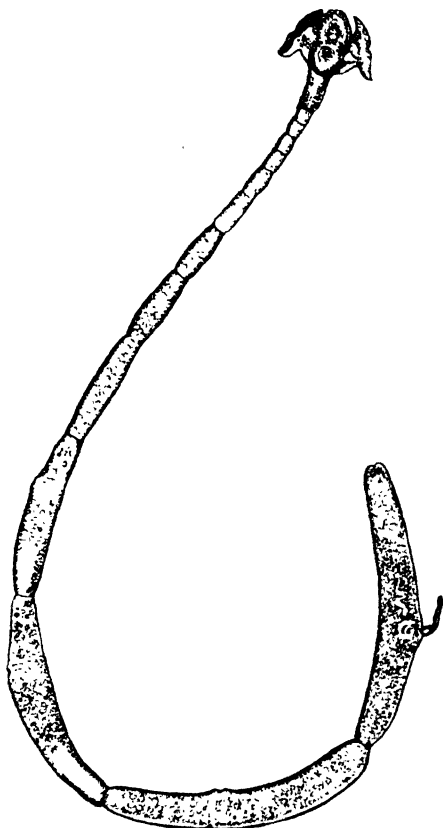


Fig. 79. – *Phyllobothrium lintoni.* Entire worm, × 8. (After Southwell.)

(8) **Phyllobothrium floriforme** (Southwell, 1912). (Fig. 80.)

Synonym :—*Anthobothrium floraformis* Southwell, 1912.

From (1) *Carcharias bleekeri* and (2) *Carcharias* sp., Pearl Banks, Ceylon. Southwell.

The worm measures 9 mm. in length, 400 μ in breadth, and

is composed of about twelve segments. The head bears four bothridia each shaped like a shallow cup; accessory suckers absent. The neck is long; the genital pores are irregularly alternate and situated laterally in the anterior third of the segment.

The writer in 1925 placed this species as a synonym of *Anthobothrium giganteum* van Beneden, 1858; subsequent examination of the species leads the writer to conclude that it is distinct.

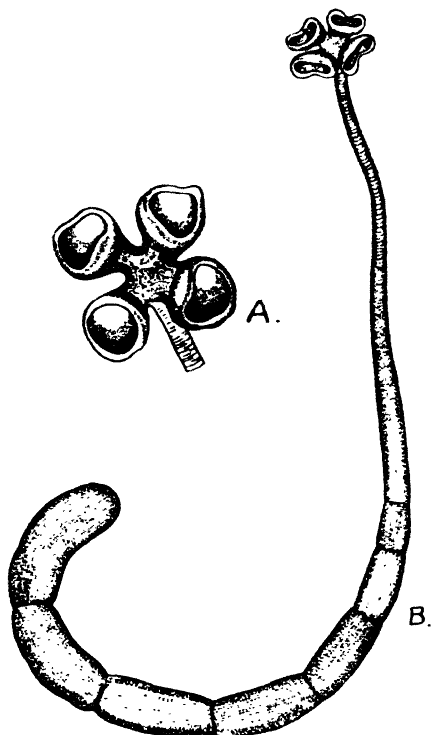


Fig. 80.—*Phyllobothrium floriforme*. A, head, ×40; B, entire worm, ×20. (After Southwell.)

(9) **Phyllobothrium tumidum** Linton, 1922. (Figs. 81 & 82.)

From *Hemigaleus balfouri*, Ceylon, Marine Biological Survey. Pearson.

The worm measures up to 9 cm. in length and 1·4 mm. in breadth. The genital pores are irregularly alternate and are situated in the anterior third of the margin of the segment. The strobila is slender and there is a short neck. The head bears a dome-shaped myzorhynchus; accessory suckers

prominent. The musculature consists of a number of inconspicuous bundles extending from just beneath the cuticle towards the median axis. Circular fibres are absent. Vitelline glands are situated laterally, internally to the longitudinal muscle bundles. Testes numerous, extending on the pore side posteriorly to the cirrus pouch. Cirrus spiny. From the ovary the vagina runs almost to the anterior extremity of the segment, then turns posteriorly, and dilates into a rather long and very wide tube.

Linton states that the eggs are discharged through a "large longitudinal opening, which opens by dehiscence on the ventral side of the ripe proglottides." The largest uterine egg measures 35 by 25 μ and bears about twelve short filaments, each measuring from 6 to 10 μ.

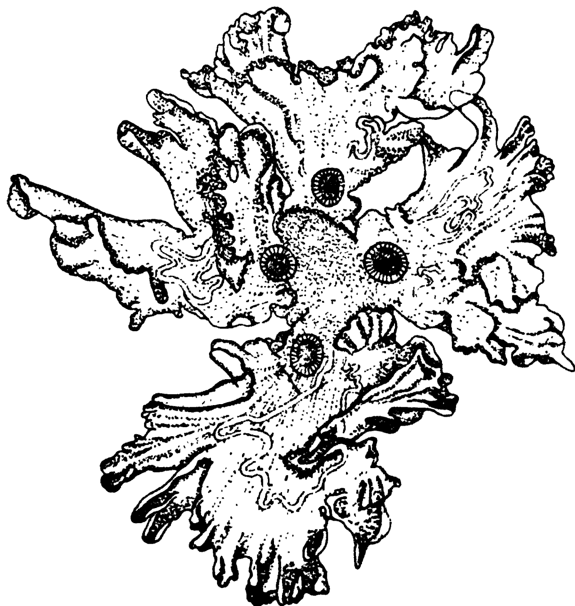


Fig. 81.—*Phyllobothrium tumidum*. Head × 16. (After Linton.)

(10) **Phyllobothrium dagnalli** Southwell, 1927. (Figs. 83, 84, & 85.)

Synonym:—*Anthobothrium pulvinatum* Southwell, 1925.

From *Rhina ancylostoma*, *Chiloscyllium indicum*, and *Galeocerdo arcticus*, Pearl Banks, Ceylon. Southwell.

In formalin the worms measure up to 18 cm. in length and the greatest breadth is 2·1 mm. In spirit they are hard and much contracted. Each is composed of several

hundred segments. There is a short neck, but for some distance (3 to 5 mm.) behind the head the segmentation is only faintly marked, even under low-power magnifications; posteriorly it becomes increasingly distinct.

The genital pores are irregularly alternate and situated near the middle of the lateral margin of the segment.

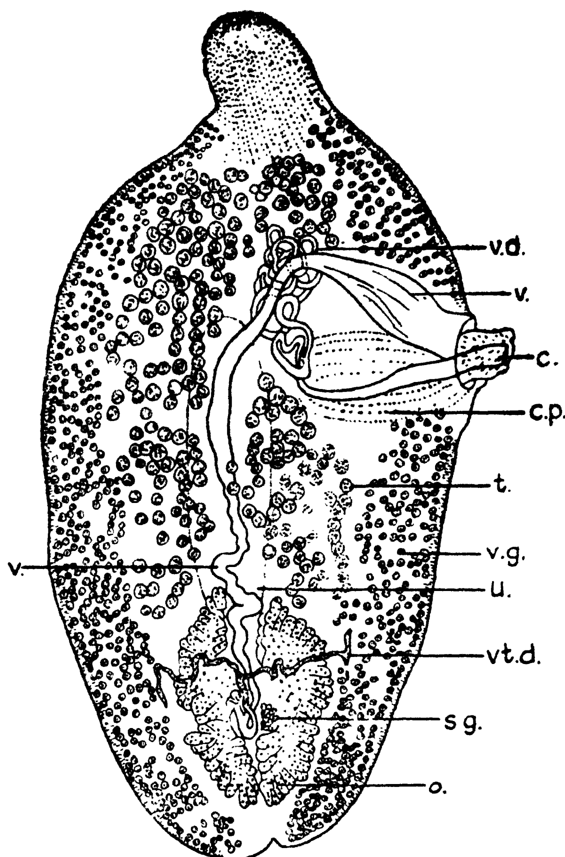


Fig. 82.—*Phyllobothrium tumidum.* Mature segment, × about 20. (After Linton.)

Ventrally, in the mature and partly gravid segments, there is an enormous uterine pore. The largest segments measured 2·2 mm. in length and 1 mm. in breadth.

Head. The surface of the head presents the appearance of a rose fully open. The individual bothridia can only be identified with difficulty, but the folds are seen to be disposed

into eight principal parts. It is concluded, therefore, that each bothridium, besides being roughly divided into two, is also folded upon itself. The margins of the bothridia are armed with minute spines. Four very small accessory suckers can be seen in mounted specimens and this fact suggests that there are four bothridia. The head is not massive and fleshy, like *P. lactuca,* but delicate and membranous in appearance. It measures about 1·7 mm. in length and 2·2 mm. in breadth. The accessory suckers have a diameter of about 150 μ and are not always easy to locate.

Details of the nervous, muscular, and excretory systems are not known.

Testes. The testes are numerous and when fully developed each has a diameter of about 60 μ ; they vary a little in shape.

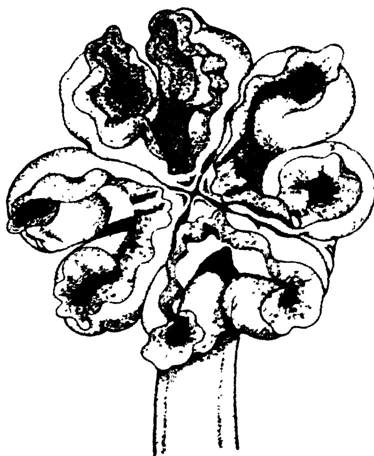


Fig. 83.—*Phyllobothrium dagnalli.* Head, viewed *en face,* × 12. (After Southwell.)

On the pore side they do not extend posteriorly to the cirrus pouch, but aporally they reach almost to the ovary. They occupy the entire field anteriorly to the cirrus pouch.

Vas deferens. The cirrus pouch is thick-walled and stretches across two-fifths the diameter of the segment and lies posteriorly to the vagina. The cirrus lies coiled and greatly enlarged within the pouch ; it is covered with spines. Outside the pouch the vas deferens is short, coiled, and lies median and anteriorly to the pouch.

Ovary and Oviduct. The ovary is situated quite posteriorly

and is lobed, but in certain segments it appeared as a single, uniformly granular mass.

The oviduct arises from the ovary, runs straight forward in the median longitudinal axis to a point in front of the cirrus pouch. It then curves sharply and runs anteriorly to the cirrus pouch to the pore. It is a very wide tube having a diameter of 70 μ throughout its length; the portion anterior to the cirrus pouch has thick granular walls.

The vitelline glands are small and lateral even in the most mature segments. Shell gland apparently absent.

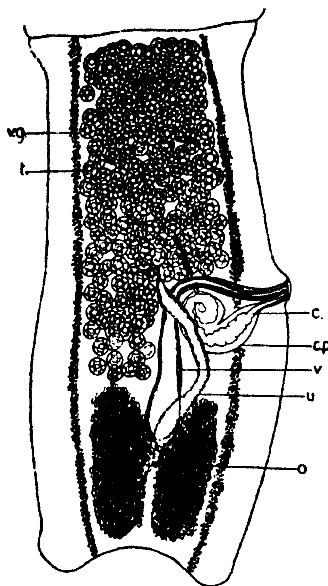


Fig. 84.—*Phyllobothrium dagnalli.* Mature segment, × 35. (After Southwell.

Uterus. This organ is rudimentary in the oldest segments and extends as a granular mass in the median longitudinal axis as far forward as the cirrus pouch. One segment was seen which contained a double set of genital organs, one set anterior to the other, the appearance being that the line of demarcation between the two segments had failed to develop.

The four species (*Anthobothrium laciniatum* Linton, 1890; *A. pulvinatum* Linton, 1890; *Phyllobothrium tumidum* Linton, 1922; and *P. dagnalli* Southwell, 1927) described above

resemble each other very closely. The points in which they differ are shown in the following table :—

	Phyllobothrium laciniatum (Linton, 1890).	*Phyllobothrium pulvinatum* (Linton, 1890).	*Phyllobothrium tumidum* Linton, 1922.	*Phyllobothrium dagnalli* Southwell, 1927.
Size	2·5 cm.	5·5 cm.	Not given (1·2 cm.?)	18 cm.
Bothridia...	Rather simple.	Very folded; in 4 lots.	Folded.	Very folded; in 4 lots,
Myzo-rhynchus.	Absent.	Absent.	Prominent.	Usually very small, rarely prominent.
Accessory suckers.	Absent.	Absent.	Present.	Present.
Neck	Long or short.	Long.	Short.	Short.
Pore...	Anterior third.	Middle.	Anterior third.	Middle.
Testes	A number behind pouch on pore side.	?	A number behind pouch on pore side.	None behind pouch on pore side.
Cirrus	Spiny.	Spiny.	Spiny.	Spiny.
Uterine pore.	?	?	Large.	Very large.
Segments ..	Sometimes laciniated.	Not laciniated.	Not laciniated.	Not laciniated.

It will be seen that *P. dagnalli* resembles *P. tumidum* closely; it differs from it, however, in (1) its larger size,

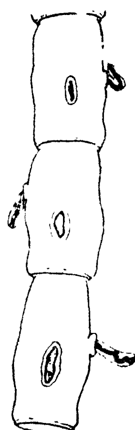


Fig. 85.—*Phyllobothrium dagnalli*. Outline of terminal segments, showing uterine pore, × 12. (After Southwell.)

(2) the position of the genital pore, and (3) in the fact that, on the pore side, no testes occur posteriorly to the cirrus pouch.

The writer in his monograph on the 'Tetraphyllidea' (1925) gave a description of the anatomy of *P. pulvinatum* (Linton, 1890) (pp. 188-190). In view of the close morphological relationships between the four species noted above, he has re-examined the material; a prolonged and careful search resulted in the finding of an accessory sucker on each bothridium, and, further, in most specimens examined no myzorhynchus could be found, but in a few this structure, of variable size, was present, whilst in one specimen only a large and prominent myzorhynchus was present.

It is therefore clear that the worms described by him (1925) under the name *Phyllobothrium pulvinatum* (Linton, 1890) are specimens of *Phyllobothrium dagnalli* Southwell, 1927

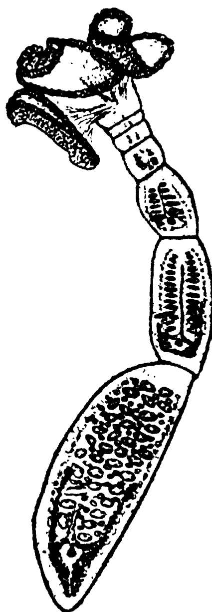


Fig. 86.—*Phyllobothrium microsomum*. Entire worm, × 38. (After Southwell and Hilmy.)

(11) **Phyllobothrium microsomum** Southwell & Hilmy, 1929. (Figs. 86 & 87)

From *Ginglymostoma concolor*, Pearl Banks, Ceylon. Pearson.

The worms are very minute and measure from 2·2 to 2·4 mm. in length; they are composed of six to seven segments, the last one being nearly as long as the rest of the worm, and measuring

about 1 mm. in length. The maximum breadth of the worm varies from 234 to 312 μ. The genital pores are difficult to locate; they are irregularly alternate and situated a little behind the middle of the lateral margin of the segment. The head consists of four unarmed, boat-shaped bothridia borne on short stalks, each having a length of about 350 μ and a breadth of 200 μ. Their margins are definitely thickened, the rim having a breadth of about 17 μ; their shape and

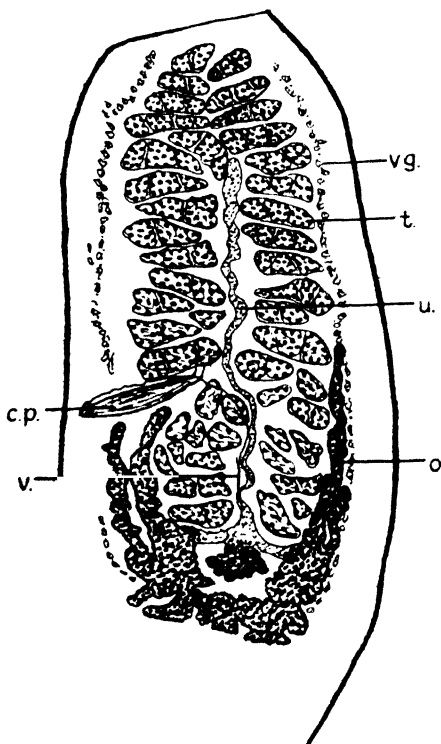


Fig. 87.—*Phyllobothrium microsomum.* Mature segment, × 190. (After Southwell and Hilmy.)

appearance vary considerably. Accessory suckers are absent, as is also a myzorhynchus. There is no neck.

Owing to lack of material, nothing is known regarding the excretory, muscular, and nervous systems.

Testes. These first appear in the second or third segment and reach their maximum development in the last; their disposition in the latter is very different from that in the other segments; thus, in the penultimate one they are arranged in capsules, these being disposed in two longitudinal rows,

one on each side of the median longitudinal axis. There are about 25 capsules on either side; they lie with their longer diameter transversely, and each measures about 50 by 16 μ. In the last segment the capsules have disappeared entirely and the testes lie free, occupying the greater part of the segment, the bilateral arrangement having been lost.

This condition obtains in quite a number of species of Tetraphyllidea, but has hitherto not been described.

The cirrus sac in the penultimate segment extends about a third the distance across, its external extremity being directed anteriorly. The vas deferens is only slightly coiled, and is situated close to the median extremity of the sac.

The ovary is U-shaped, each limb being bifid; the aporal limbs are slightly longer than the poral and extend along the lateral margin almost to the middle of the segment.

The vagina is a simple thick-walled tube which, from the pore, runs anteriorly to the cirrus sac. The vitelline glands consist of two rows of acini, one running along and close to each lateral margin of the segment.

The shell gland is prominent and situated in the concavity of the ovary; it measures 25 by 31 μ. Immediately anterior to it can be seen the two oviducts, one from each ovarian limb, which meet in the middle line. They are continuous with the vagina and the uterus.

Uterus. Only the rudiment of this organ could be seen, and this consisted of a granular condensation resembling a tube running along the median longitudinal axis.

As in practically all other species of this family, gravid segments and eggs are unknown.

Species inquirendæ.

(12) **Phyllobothrium pammicrum** Shipley & Hornell, 1906. (Fig. 88.)

From *Carcharias melanopterus*, Pearl Banks, Ceylon. Hornell.

The worm measures from 1·1 cm. to 1·3 cm. in length; the greatest breadth is about 500 μ. The head and neck are very transparent. The former carries four sessile bothridia, the edges of which are decidedly crumpled; there are no areolæ. Numerous muscles traverse the long neck.

The segmentation is peculiar. There is no sign of the gradual differentiation of the proglottis, first as a narrow band which broadens as it passes backward; on the contrary, the most anterior segment is almost as large as the posterior ones. The proglottides have straight parallel margins which are not salient. The genital pores are unilateral. The posterior segments are at least three times as long as broad.

In 1925 the writer placed this species as a synonym of *Phyllobothrium giganteum* van Beneden, 1850. Its identity is doubtful.

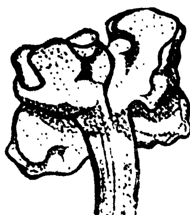


Fig. 88.—*Phyllobothrium pammicrum.* Head, × 70. (After Shipley and Hornell.)

(13) **Phyllobothrium blakei** Shipley & Hornell, 1906. (Fig. 89.)

From *Dasybatus kuhli*, Pearl Banks, Ceylon. Hornell.

"They are very delicate, thin, fragile creatures measuring 10 mm. in length and at their greatest width from 250 to 330 μ.

"The head measures over 500 μ. It consists of four crumpled bothridia with thickened edges, which are so twisted



Fig. 89.—*Phyllobothrium blakei.* Head, × about 50. (After Shipley and Hornell).

that they show numerous little bays and rounded recesses which at first sight might easily be taken for small circular suckers. These bothridia spring with practically no stalk from the edge of a hollow which shows some circularmarkings, as if there were here two rings of circular muscles. There is no kind of armature.

"The proglottides immediately following the head are broader than the subsequent ones; they soon, however, narrow, and only very slowly widen again. The sides of the proglottides are straight and almost parallel, and, although they project very slightly at their hinder end, they do not overlap the succeeding segment. The posterior proglottides are almost three times as long as they are broad, and instead of having square ends they have rounded ones, and are swollen in the middle. Their contents seem to be a roomy uterus with numerous large ova. The reproductive pores are alternate." (*Shipley & Hornell.*)

Genus II. ECHENEIBOTHRIUM van Beneden, 1850.

Synonyms:—*Bothriocephalus* of Rudolphi, Leuckart, Bremser, Dujardin, etc.
Rhinebothrium Linton, 1889.
Tiarabothrium Shipley & Hornell, 1906.

Van Beneden in 1850 described the genus *Echeneibothrium* as follows:—" The four bothridia are placed on long protractile stalks; they vary extraordinarily in form, and are characterized by regular grooves which develop over the entire length of these organs, and which make them appear like the suckers of an *Echeneis*. Type-species:—*Echeneibothrium minimum* van Beneden, 1850."

Bremser in 1824 figured Rudolphi's species *B. tumidulus*.

It appears almost certain from the figures of *B. tumidulus* Rud. and *B. echeneis* Leuckart that the two species are identical with *E. variabile* van Ben., 1850. One of Leuckart's figures suggests that he also had in his collection a specimen of a worm which van Beneden later on described as *Phyllobothrium lactuca*.

Dujardin in 1850 considered that the above species were identical, and he retained the name *B. tumidulus*, adding the following description:—" Length 10 mm. to 160 mm., and 0·5 mm. to 1 mm. in breadth. Head 1·5 mm. to 2 mm. broad, with four distinct bothridia, in the shape of oval lobes, divided into numerous transverse areolæ, and also further divided by a longitudinal partition into two parts. The first segments are almost rectangular, sometimes contracted and short, sometimes elongated. The last segments are rounded and more distinct; the ovary forms two brownish patches near the posterior edge. In the intestine of *Torpedo marmorata* and *Raja pastinaca*. Leuckart has described the principal modifications of shape in the bothridia, which are sometimes almost united into a globular mass, sometimes each divided into two petal-like lobes bearing areolæ, etc."

In 1863 Diesing described the characters of the genus

Echeneibothrium as follows :—" Body elongated ; head continuous with the body, or with a separate neck ; there is a terminal, retractile myzorhynchus and four bothridia facing each other, each bothridium bearing transverse areolæ, sometimes divided by a longitudinal partition. The posterior border of each bothridium is continuous with a contractile and mobile peduncle fixed on the head. An os is present on the apex of the myzorhynchus. Genital pores marginal."

Linton (1899) separated those species which had characteristic echeneiform bothridia, but were destitute of a myzorhynchus, from the genus *Echeneibothrium*, and placed them in *Rhinebothrium*, which he defined as follows :—" Body articulate. Head continuous with the body or separated by a neck, merging into segmented body, or separated by a constriction. Bothria four, opposite, or in lateral or marginal pairs, faces divided into loculi by several or many transverse and one or few longitudinal muscular partitions mounted on slender pedicels, very versatile, unarmed ; myzorhynchus none. Genital apertures marginal."

It will be noted that in van Beneden's original description no mention is made of a myzorhynchus. Braun states that the myzorhynchus is generally long and powerfully developed, but that it may abort in old age. The writer accordingly considers that the genus *Rhinebothrium* is synonymous with *Echeneibothrium*, the latter having priority.

Braun (1900) defined the characters of the genus *Echeneibothrium* as follows, and divided it into two subgenera—*Discobothrium* van Ben., 1871, and *Rhinebothrium* Linton, 1889 :—" Scolex with four long stalked bothridia, very mobile, whose inner surface is divided by one or two longitudinal and numerous transverse septa into two or three longitudinal series of areolæ. When stretched, or strongly contracted, the areolæ may disappear. Pores alternating. Anterior myzorhynchus generally long and powerfully developed, but may abort in old age. Neck short or absent. Cirrus spiny."

In another part of this volume the writer gives reasons for considering the genus *Discobothrium* distinct from the genus *Echeneibothrium*. Braun (1900) concludes that in *Echeneibothrium* (1) the areolæ may disappear, (2) the anterior myzorhynchus may abort in old strobilæ, (3) the neck is short or absent, and (4) the cirrus is spiny.

Diesing states that there is a terminal os at the apex of the myzorhynchus, and that the genital pores are marginal.

Beauchamp (1905) erected the tribe Echeneibothrines, in which he included the genera *Echeneibothrium* and *Discobothrium*. He agreed that the characters of the genus *Echeneibothrium* were well defined, but pointed out that " when the question of species arises, difficulties begin, and whoever has

seen living examples of these animals will understand that a specification is practically impossible (see van Beneden's drawings). Neither the number of loculi, which is perhaps fairly constant (but regarding which mistakes can be easily made, as I will show), nor the general shape of the bothridia, nor the presence or absence of a myzorhynchus (on which Linton has founded his genus *Rhinebothrium*) are characters above criticism. Finally, the length of the neck and the law of the growth of the segments are . . . characteristics of a variety, or of an individual, rather than of a species. It thus follows that in the genus there is, perhaps, not a single species which can be clearly differentiated from the others. Without speaking of Linton's species, certain authors have united, under the name *E. tumidulum*, the *E. variabile* and *E. minimum* of van Beneden, which nevertheless seems fairly distinct. *E. sphæricephalum* Diesing has been identified with *E. variabile*, and *E. affine* Olsson with *E. dubium* van Ben., of whose individuality one of my observations might make me doubtful . . . . In Banyuls I found two forms that seemed distinct, although I would not absolutely affirm this. The most common of these I identify with *E. variabile*, although it differs from this species in several ways. The other did not seem to me to fit in with the description of any species, but I would not venture to create a new species."

The author is fully in agreement with the above remarks.

The characters of the genus *Echeneibothrium* are emended as follows :—The four bothridia are either sessile or pedunculated ; they vary extraordinarily in form, but are generally characterized by regular grooves which develop over the entire surface of these organs, and which make them appear like the suckers of an *Echeneis* ; genital pore marginal. Type-species :— *Echeneibothrium minimum* van Beneden, 1850.

Key to Species.

1. Bothridia Y-shaped owing to half of each being split longitudinally into separate parts	*E. trifidum*, p. 225.
Bothridia not so divided	2.
2. Bothridia split into two halves, due to the presence of a transverse hinge	*E. flexile*, p. 218.
Bothridia not divided by a transverse hinge.	3.
3. Faces of bothridia split into a series of transverse loculi, not divided longitudinally	*E. minimum*, p. 212.
Faces of bothridia divided into three longitudinal rows of loculi	*E. cancellatum*, p. 223.
Faces of bothridia typically divided into loculi by numerous transverse and a single longitudinal septum ; extremely variable in form	*E. tumidulum*, p. 215.

(1) Echeneibothrium minimum van Ben., 1850. (Figs. 90, 91, & 92.)

Synonyms :—*E. trygonis* Shipley & Hornell, 1906.
Tiarabothrium javanicum Shipley & Hornell, 1906.
Rhinebothrium shipleyi Southwell, 1911.
? *Anthobothrium ceylonicum* Southwell, 1912.

From (1) *Rhinoptera javanica*, (2) *Dasybatus walga* and *D. kuhli*, Pearl Banks, Ceylon. Hornell ; Southwell. (3) *Carcharias* sp., India. Pearson.

"Strobila 15 mm. to 17 mm. in length, and so fine that it can hardly be seen with the naked eye. It consists of not more than 15 segments, the first segment being nearly square and the last five or six times longer than broad. The bothridia are divided into eight or ten areolæ which can be separated in the middle. The adult worm is distinguished by the long stiff spines at the base of the cirrus. The male pore opens laterally

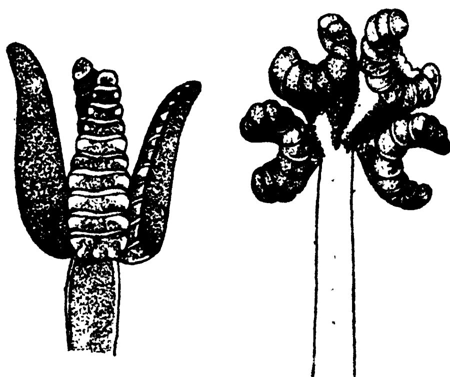


Fig. 90.—*Echeneibothrium minimum.* Heads, magnification unknown. (After van Beneden.)

near the middle. There are four mobile bothridia which are very variable in shape ; they are pedunculated. Myzorhynchus not pronounced. There are folds all along the length of the bothridia, and sometimes these are divided in the middle by a deep furrow. Eight or ten areolæ may be seen. The pores are alternate. The cirrus may be half the length of the body ; it is armed with small spines, and its base is swollen and armed with very large spines. The vaginal pore lies anterior to the cirrus pouch. In gravid segments the genital pore may be situated posteriorly.

"The species is very similar to *Bothriocephalus echeneis* Leuckart, but differs from it (1) in being smaller, (2) in the

absence of a neck, and (3) by having fewer segments. *Bothriocephalus tumidulus* Rud. is not exactly like *B. echeneis.*" (*van Beneden.*)

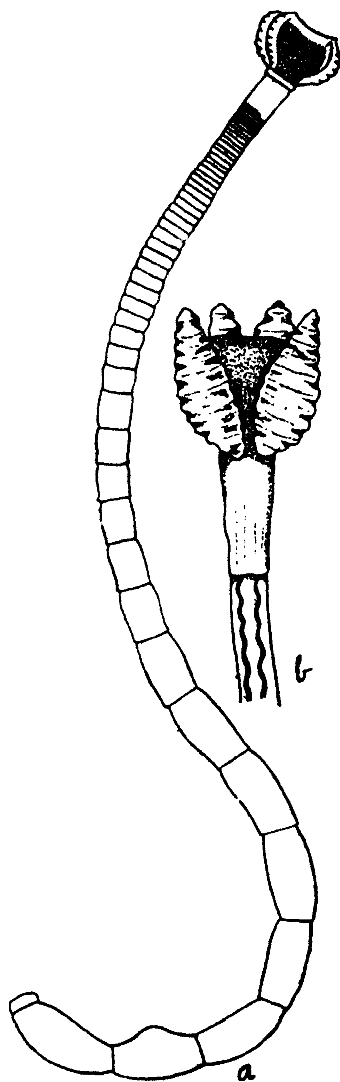


Fig. 91.—*Echeneibothrium minimum.* a, entire worm, × 16; b, head, × about 50. (After Shipley and Hornell.)

Echeneibothrium trygonis Shipley & Hornell, 1906.

"The worm measures from 8 mm. to 15 mm., and the head has a width of nearly 1 mm. The neck passes into the head like the stem of a goblet into the bowl, so that the bothridia are not pedunculated. The inner face of each bothridium bears seven or eight areolas stretching across the bothridium, and thus there is no median longitudinal line. There is a stout neck broader than the succeeding segmented part. The posterior segments are about five times as long as broad. Pores ?" (*Shipley & Hornell.*)

This species is inseparable from *E. minimum* van Ben.



Fig. 92.—*Echeneibothrium minimum.* a, head, viewed *en face.* × 10; b, a bothridium, × 16. (After Southwell.)

Tiarabothrium javanicum Shipley & Hornell, 1906.

The characters of the genus *Tiarabothrium* are:—"About 11 mm. to 12 mm. long. Head with four sessile bothridia, each divided into twelve transverse areolas: the bothridia can be raised off the head anteriorly. Two stout muscles enter the head laterally and split up into four muscles on each side, two of which are inserted into each bothridium. Definite neck present, provided with an extensile collar. Proglottides with slightly concave sides, divided from each other by perfectly flat partitions. Genital pores alternate. Penis with numerous spines." (*Shipley & Hornell.*)

The genus *Tiarabothrium* is clearly synonymous with *Echeneibothrium*, from which it is said to differ only in having the bothridia sessile instead of pedunculated. The species *T. javanicum* appears to be indistinguishable from *E. minimum* van Ben., except that in the former there is, according to some authors, a well-developed myzorhynchus.

Rhinebothrium shipleyi Southwell, 1911. (Fig. 92.)

"The head consists of four bothridia borne on long, triangular, flattened, and very versatile stalks. The face of each both-

ridium is long and narrow, and is divided by transverse septa only into ten unpaired areolæ. There is no longitudinal septum. Each bothridium is 1 mm. long and approximately 0·3 mm. broad. The ends are rounded, and the whole bothridium is fringed with a delicate irregular membrane. In the contracted state the bothridia are often roughly semicircular in shape, with the areolæ either on the concave or the convex surface. The breadth of the head varies with the state of contraction and with the disposition of the bothridia, but averages about 1·8 mm. There is no myzorhynchus. Immediately posterior to the head is a swollen bulbous portion, triangular in shape, with the apex passing into the proglottides. There is no neck, although the first few transverse divisions between the proglottides are faint and indistinct. The first segments are shallow, 0·3 mm. in breadth, and much broader than long, and they continue so up to the last few (6 to 8) ripe segments, which latter are square, and then slightly longer (1·2 mm.) than broad (0·9 mm.) The largest of our specimens was 60 mm. long and the smallest 42 mm. Most specimens were whip-like in appearance, the maximum breadth being attained at a distance of about 30 mm. from the head, and they continued the same breadth to the end. This anterior part of the worm is apt to be of uneven breadth, which fact is doubtless due to irregular contraction. The posterior and ripe proglottides are of varying shades of a dark brown colour. The genital pores are lateral and irregularly alternate. In some specimens the edges of the proglottides in the middle region of the worm were slightly salient." (*Southwell*).

This species only differs from *E. minimum* in being larger and composed of a much larger number of segments. Van Beneden definitely stated that in *E. minimum* not more than fifteen segments were present. In spite of this fact the writer considers that the two forms are identical, as in each case the head bears only transverse areolæ.

(2) **Echeneibothrium tumidulum** (Rud., 1819). (Figs. 93, 94, & 95.)

Synonyms :—*Bothriocephalus tumidulus* Rud., 1819.
Bothriocephalus echeneis Leuckart, 1819.
Echeneibothrium variabile van Ben., 1850.
Echeneibothrium ceylonicum Shipley & Hornell, 1906.

From *Dasybatus walga*, Pearl Banks, Ceylon. Hornell.

Rudolphi in 1819 gave a brief description (but no figure) of a worm from *Raja pastinaca* which he named *Bothriocephalus tumidulus*, and which measured about half an inch in length. It is difficult to identify this species, but it apparently belonged to the genus *Echeneibothrium*. Rudolphi's description of

he worm is as follows :—" Each bothrium has two oval, not very thick, divisional lines, with transverse stripes. Neck very short. First segments very narrow and elongated, the following ones subquadrate."

Bremser sent to Rudolphi a worm which measured 5 lines

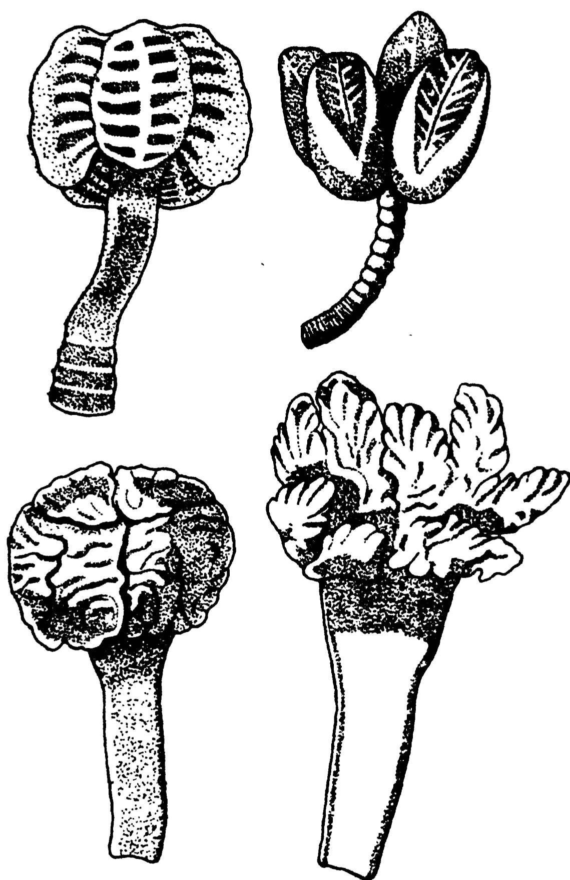


Fig. 93.—*Echeneibothrium tumidulum*. Heads, magnification unknown. (After Leuckart.)

in length. " In the head each bothridium has two ridges, each of which is divided by a single elevated median line in the longitudinal axis. The rest is divided by three transverse stripes. Neck short and narrowing posteriorly. First segments narrow and elongated, the following ones are broader and shorter, subquadrate, with obtuse angles. The head

was unarmed; the bothridia have a transverse ridge with stripes, placed regularly, but some differ from others." Bremser's figure of this species is reproduced in fig. 94.

In 1819 Leuckart described *Bothriocephalus echeneis* from the same host and gave figures (fig. 93).

Fig. 94.

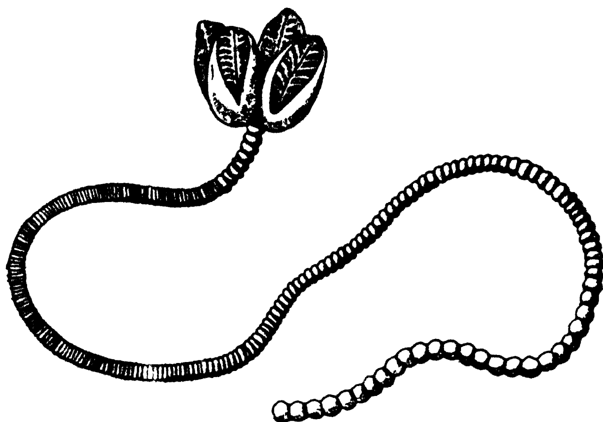
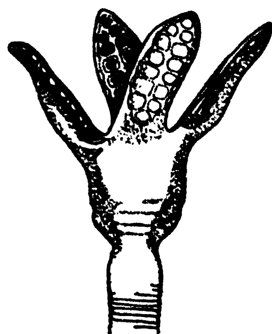


Fig. 95.



Echeneibothrium tumidulum.

Fig. 94.—Entire worm, magnification unknown. (After Bremser.)
Fig. 95.—Head, magnification unknown. (After Shipley and Hornell.)

Echeneibothrium ceylonicum Shipley & Hornell, 1906.

"Length from 8 mm. to 2·5 cm. Head small, splitting up into four short arms or bothridia each bearing 14 areolæ, there being a terminal one at each end and six pairs. Body

stout; neck present. Lateral margins of segment convex. The reproductive pore is median." (*Shipley & Hornell.*)

This species is indistinguishable from *E. tumidulum* (Rud., 1819). The presence of a median reproductive pore is, however, unusual. Zschokke observed a similar condition in *E. myliobatis aquilæ*, but concluded that the appearance was due to torsion of the segment.

(3) **Echeneibothrium flexile** (Linton, 1890). (Figs. 96, 97, 98, & 99.)

Synonyms:—*Rhinebothrium flexile* Linton, 1890.
Echeneibothrium walga Shipley & Hornell, 1906.
Echeneibothrium insignia Southwell, 1911.

From *Dasybatus walga* and *D. uarnak*, Pearl Banks, Ceylon. Hornell; Southwell.

"Bothria four, opposite, long, slender, versatile, attached at middle point to head by moderately short pedicels. Face of each bothrium with numerous loculi in two longitudinal rows, forty, more or less, in each row. The slender, free ends of the bothria very versatile, bending readily in any direction, but especially in the plane of the supporting pedicel and axis of the body. An apparent hinge in middle of face of each bothrium opposite the pedicel. No head, strictly speaking, except what is formed by the bothria and their pedicels. Myzorhynchus none. Neck short, cylindrical, merging imperceptibly into the body. Segments begin near the head. First distinct segment broader than long, very soon becoming squarish, then longer than broad; mature segments six or eight times as long as broad, subcylindrical or fusiform, narrowed at the extremities. Genital apertures marginal, about middle of segment; cirrus echinate. Maximum length 16 mm.; length of posterior segments from 1 to 1·6 mm., breadth 0·2 to 0·32 mm. Habitat:—*Trygon centrura*, spiral valve, twenty-five specimens, Wood's Holl, Massachusetts, August 10, 1887. . . . . *E. minimum* is characterized by having the bothria crossed by eight or ten transverse septa, while *R. flexile* has in the neighbourhood of forty. . . ." (*Linton.*)

The hinge in the middle of the face of each bothridium appears to differentiate this species from all others of the genus *Echeneibothrium.*

Echeneibothrium walga Shipley & Hornell, 1906.

A single specimen was obtained by the above authors, and this measures 7 mm. in length and about 200 μ in breadth. The posterior segment was said to be ripe and the animal probably fully grown. The head breaks up into four long

stalks each bearing two bothridia or rather two halves of a bothridium. The stalks measure about 1 mm. Each half of the bothridium bears a double row of some twelve areolæ (total twenty-four), which are not rounded off towards the longitudinal median partition. Neck very short; cirrus

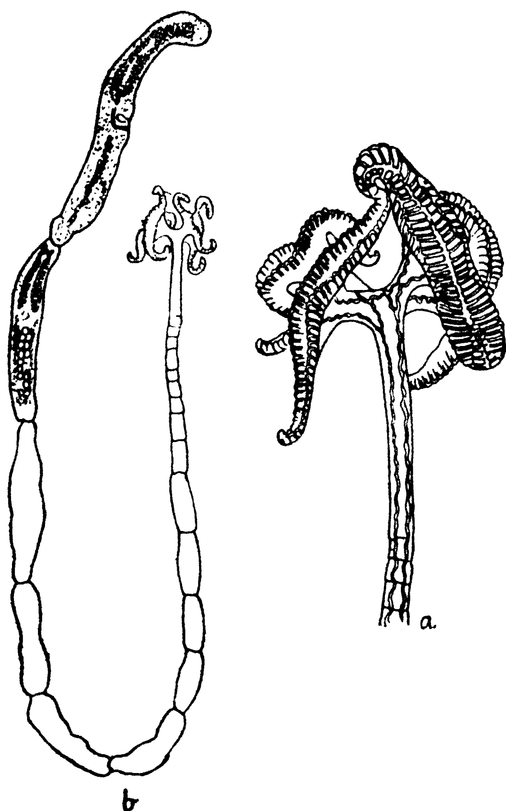


Fig. 96.—*Echeneibothrium flexile*. *a*, head, × 45; *b*, entire worm. × 22. (After Linton.)

spiny; genital pores apparently regularly alternate. The species is characterized by having each bothridium hinged in the middle, and is indistinguishable from *E. flexile* (Linton. 1890).

Echeneibothrium insignia Southwell, 1911.

Delicate worms 3 cm. in length; the head measures 1·4 mm. across when fully expanded, and bears four leaf-like bothridia; each bothridium is constricted on both sides of its long axis.

About eighty segments were counted, and the posterior ones were not ripe.

The type specimen of *E. insignia* and three others from *D. kuhli* have been carefully re-examined by the author, who is now of opinion that the worm is probably identical with *E. flexile* Linton, 1890, in spite of the difference in size. The anatomy of this species has not been described, and it is unfortunate that in only one specimen were mature proglottides found, and these were so badly preserved that it was impossible to make out the finer details of their morphology.

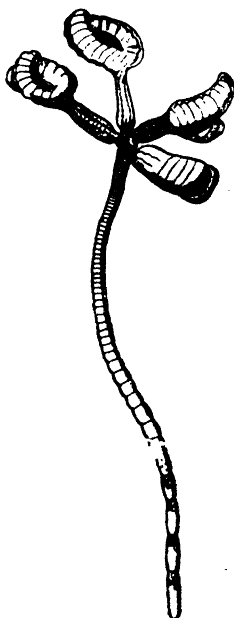


Fig. 97.—*Echeneibothrium flexile.* Entire worm, × 13. (After Shipley and Hornell.)

Head. The peduncles of the bothridia vary very much in length; sometimes they are very long indeed, whilst at other times the bothridia appear almost sessile. The number of loculi on the bothridia also varies from about twenty-six to thirty-eight, and whilst the longitudinal septum was clearly visible in most bothridia, it could not be seen in others. Thus in one worm one bothridium was divided longitudinally and three bothridia were apparently undivided. In the latter case the loculi had the appearance of being transverse and undivided

as they are in *E. minimum*, but *E. insignia* differs from *E. minimum* in having each bothridium hinged in the middle. The neck also varies in length within wide limits; in two specimens it was very long and in two others (young) it was very short.

Testes and Vas deferens. There are from about eighteen to twenty-six testes; at first they are arranged in two lateral

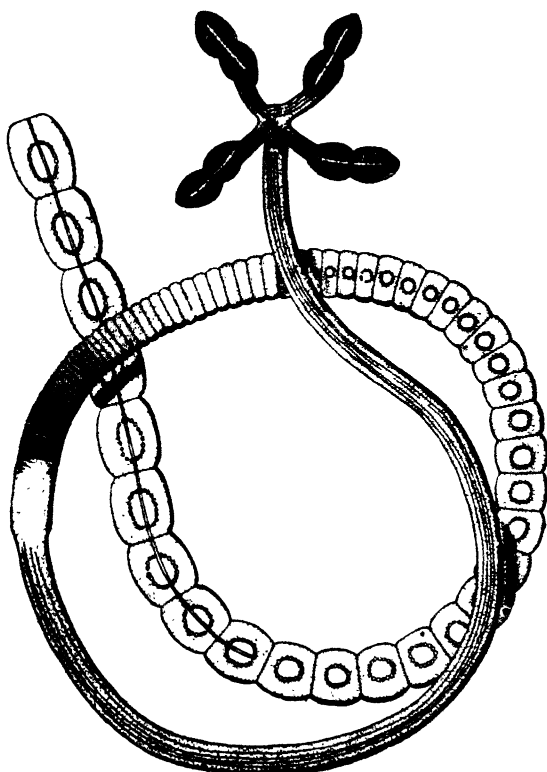


Fig. 98.—*Echeneibothrium flexile.* Entire worm, × 20. (After Southwell.)

rows, one on each side of the median line. The cirrus pouch lies posteriorly to the vagina and is cylindrical in shape, extending almost to the longitudinal axis of the segment. The cirrus is club-shaped, and appears to be devoid of spines. On leaving the cirrus pouch the vas deferens forms a coil near the antero-posterior axis of the segment and anteriorly to the cirrus pouch. The fully mature segments are about four times as long as broad, and in these the cirrus pouch

becomes bent posteriorly. The genital pore lies in the anterior half of the segment.

Ovary and Vagina. In full development the ovary occupies the posterior quarter of the segment and is bilobed and very prominent. The vagina is a wide tube situated anteriorly to the cirrus pouch. From the pore it runs straight to the median antero-posterior axis and then turns posteriorly; it then narrows and follows a sinuous course to the mid-ovarial region, dilating into a small receptaculum seminis.

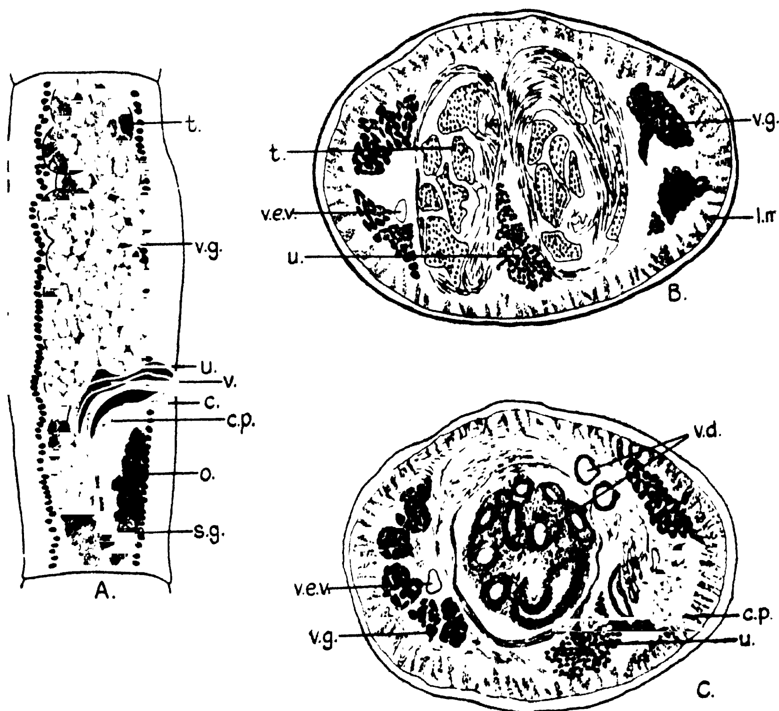


Fig. 99.—*Echeneibothrium flexile.* A, mature segment, × 125; B, transverse section of mature segment about region of testes; C, transverse section of mature segment through cirrus pouch, × 480. (Orig.)

Shell Gland. This is a very small granular organ situated between the lobes of the ovary.

Vitelline Glands. These consist of two strips of glandular tissue, one lying parallel to each lateral margin.

Uterus. The rudimentary uterus consists of a cylindrical mass of granules running in the antero-posterior axis. Eggs unknown.

(4) **Echeneibothrium cancellatum** (Linton, 1890). (Fig. 100.)

Synonyms :—*Rhinebothrium cancellatum* Linton, 1890.
Echeneibothrium javanicum Shipley & Hornell, 1906.

From *Rhinoptera javanica*, Pearl Banks, Ceylon. Hornell.

"Head with four lateral bothria which are elliptical and mounted on short pedicels ; faces of bothria with about twenty-five loculi, arranged somewhat trilineally ; anterior margins

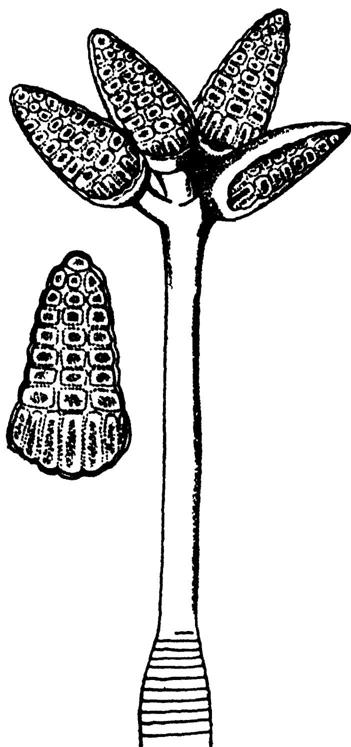


Fig. 100.—*Echeneibothrium cancellatum.* Head and neck, and a bothridium greatly enlarged ; magnification unknown. (After Shipley and Hornell.)

of bothria free, slightly projecting, posterior margins appressed, neck broad and flat at base of bothria, somewhat constricted behind head and almost immediately crossed by fine, closely-crowded, transverse lines ; distinct segments make their appearance 1 mm. or less back of head ; the segments are much broader than long throughout the length of the strobile until near the posterior end, where they are as long or even longer than broad ; they are convex on the margins, so that

the marginal outline of the strobile is crenulate ; the chain of posterior segments is rather moniliform ; the anterior and median parts of the body are crossed at more or less regular intervals by distinct transverse lines which give rise to the deceptive appearance of elongated, transversely wrinkled bothria ; body rather flat and thin ; length 25 mm. ; breadth 1 to 1·5 mm. ; genital apertures marginal, cirrus echinate." (*Linton.*)

The presence of three rows of loculi on the face of each bothridium differentiates this species from all others within the genus.

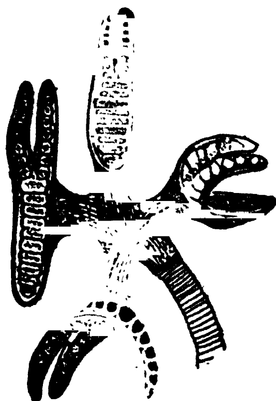


Fig. 101.—*Echeneibothrium trifidum.* Head, magnification unknown. (After Shipley and Hornell.)

Echeneibothrium javanicum Shipley & Hornell, 1906.

"Length from 9 to 12 mm. Neck one-third to one-half body length. The head is 1 mm. broad and consists of four pedunculated pad-like bothridia, somewhat triangular in shape. Each is traversed by two longitudinal and a number of transverse ridges separating the surface into a number of areolas, one of which is apical. At the base of each bothridium there are seven areolas, and these are followed by seven rows of three, the central row being ended by the apical areola. The bases of the four bothridia fuse together. Myzorhynchus absent. Neck and strobila striated. In the ripe proglottid the central uterus and the lateral yolk glands take the form of a coil with three limbs. The genital pores are lateral and alternate in pairs ; the cirrus is armed." (*Shipley & Hornell.*)

The writer considers this species identical with *E. cancellatum* (Linton, 1890).

(5) Echeneibothrium trifidum Shipley & Hornell, 1906. (Fig. 101.)

From *Dasybatus walga*, Pearl Banks, Ceylon. Shipley and Hornell.

"Worms 6 mm. or 7 mm. in length. The head bears four leaf-like bothridia, stalked and very mobile. The basal or posterior half of each bothridium is single and carries nine transversely elongated areolas. The proximal end of each bothridium is, however, split into two halves, and each half bears nine rounded areolas. There are thus, altogether, twenty-seven areolas, viz., nine large and eighteen small.

"The bothridia are pedunculated. There is no myzorhynchus. The genital pores are lateral and irregularly alternate." (*Shipley & Hornell.*)

Nothing is known of the anatomy of this species The form of the bothridia separates it from all others within the genus.

SPECIES INQUIRENDA.

Echeneibothrium simplex Shipley & Hornell, 1906, is apparently a synonym of *Phyllobothrium variabile* (Linton, 1889).

Genus III. **MYZOPHYLLOBOTHRIUM** Shipley & Hornell, 1906.

Synonym :—*Rhoptrobothrium* Shipley & Hornell, 1906.

The emended diagnosis of this genus is as follows :—The head consists of four leaf-like bothridia, pedunculated or sessile ; the terminal portion of each bothridium may be differentiated as an areola. Myzorhynchus present, bearing four suckers.

Myzophyllobothrium rubrum Shipley & Hornell, 1906. (Figs. 102, 103, & 104.)

Synonym :—*Rhoptrobothrium myliobatidis* Shipley & Hornell, 1906.

From *Stoasodon narinari* and *Ætomylæus maculatus*, Pearl Banks, Ceylon. Hornell ; Southwell.

Shipley and Hornell's specimen measured 8 cm. in length and about 400 μ in breadth ; the head measured 1 mm. in breadth and consisted of a terminal myzorhynchus which carried four almost terminal suckers ; the myzorhynchus is flanked by four sessile bothridia bearing at their apex a small thickening (? sucker) ; neck practically absent. The last few segments, which were ripe but not gravid, measured about 1·5 mm. in length and 400 μ in breadth. The edges of the proglottides are practically straight and not salient ; the genital pores are

Uterus. The rudimentary uterus consists of a solid granular mass extending from the ovary to the level of the cirrus pouch. Eggs unknown.

Rhoptrobothrium myliobatidis Shipley & Hornell, 1906. (Fig. 104.)

The genus *Rhoptrobothrium* Shipley & Hornell, 1906, was defined as follows :—" Minute forms ; head with four bothridia surrounding a myzorhynchus which carries four suckers. Bothridia stalked and leaf-like, with the terminal end cut off

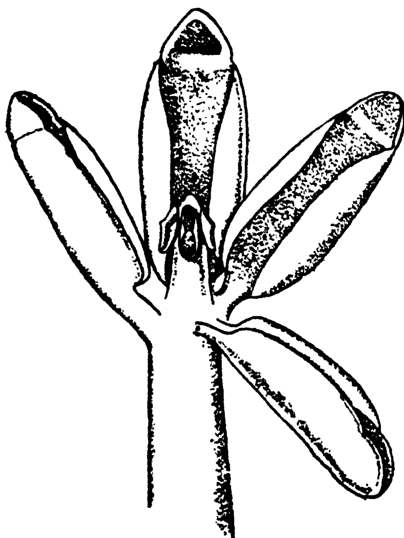


Fig. 104.—*Myzophyllobothrium rubrum.* Head, × 66. (After Shipley and Hornell.)

and forming an areola. Head extends behind the insertions of the stalk of the bothridia and is followed by a neck." (*Shipley & Hornell.*)

Type-species :—*Rhoptrobothrium myliobatidis* Shipley & Hornell, 1906.

This worm appears to be an immature form of *M. rubrum* Shipley & Hornell, 1906. Only one specimen was obtained by these authors, "and that included little more than a head." The anatomy of the species is not known, but the presence of four suckers on the myzorhynchus suggests the probability of the worm being identical with *M. rubrum* Shipley & Hornell, 1906.

Genus IV. **CARPOBOTHRIUM** Shipley & Hornell, 1906, emended.

Body segmented; head with four bothridia, each bothridium being Y-shaped; the proximal portion is somewhat cylindrical, and from its distal extremity two flaps arise, apposed to each other. The margins of these flaps may be loculated or not, and they may bear muscular pads at their point of origin. Accessory suckers and a myzorhynchus may be present or absent. Genital pores and vitelline glands marginal. Parasitic in elasmobranchs.

Type-species:—*Carpobothrium chiloscyllii* Shipley & Hornell, 1906.

Carpobothrium chiloscyllii Shipley & Hornell, 1906. (Figs. 105 & 106.)

Synonym:—? *Anthobothrium laciniatum* var. *brevicolle* Linton, 1889.

From *Rhynchobatus djiddensis*, *Urogymnus asperrimus*, and *Chiloscyllium indicum*, Pearl Banks, Ceylon. Hornell; Southwell.

The worms measure about 10 mm. in length and the maximum breadth is about 400 μ; they are composed of from 18 to 25 segments, of which only about the last three are mature. No gravid proglottides were observed. The largest one measured 4 mm. in length and 400 μ in breadth. The genital pores are irregularly alternate and are situated near the middle of the lateral margin. There is a short neck measuring about 450 μ.

Head. The head consists of four peculiar bothridia, each having the form of the letter Y; the proximal portion is somewhat cylindrical, and from its distal extremity two flaps arise, each having entire margins; but the periphery of each flap is marked by a single row of minute areolæ which run along the margin of that face of the bothridium apposed to the other bothridium in each pair. Where the two flaps arise there are a pair of very conspicuous muscle-pads, one on each flap. There is no myzorhynchus and accessory suckers are absent. The breadth and length of the head varies according to the state of contraction, but in specimens in which the head was preserved in an expanded condition it measured 1·5 mm. in breadth and from 500 to 800 μ in length.

No details are known regarding the muscular, excretory, and nervous systems.

Testes. These vary in number from about 100 to 150; they lie two, and sometimes three, abreast on each side of the vagina and about five abreast anteriorly to the cirrus pouch. When fully developed each has a diameter of about 45 μ.

Vas deferens. The cirrus pouch lies posteriorly to the vagina; it is almost globular, and extends more than halfway across the segment, pushing the uterus towards the aporal margin. The cirrus is spiny; a number of coils of the vas deferens lie within the sac. Outside it the vas deferens runs anteriorly as a much coiled tube. Seminal vesicle apparently absent.

Ovary. This is a bilobed organ situated posteriorly and composed of a number of large, irregularly shaped acini. It varies in shape considerably, each lobe being elongated when the segment is extended, and becoming shorter antero-posteriorly when the proglottid is contracted.

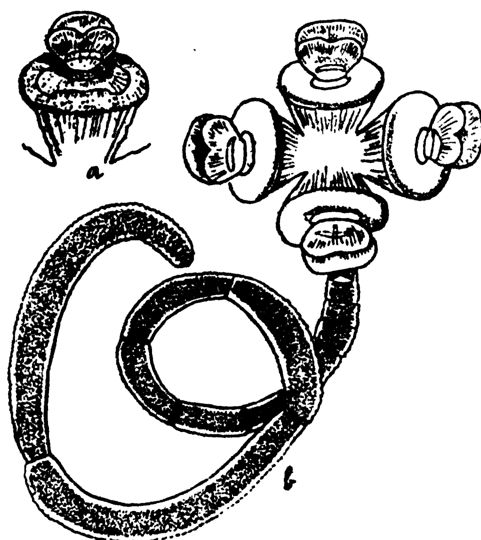


Fig. 105.—*Carpobothrium chiloscyllii.* *a*, a bothridium, × 150; *b*, entire worm, × about 100. (After Shipley and Hornell.)

Vagina. From the pore the vagina runs anteriorly to the cirrus pouch, and that portion of the vagina in front of the sac is dilated. At the median extremity of the latter it turns sharply and runs backwards in the middle line to the ovary, dilating near the latter organ into a pyriform receptaculum seminis.

Oviduct. The oviduct is very long and opens to the uterus opposite the genital pore.

Shell Gland. This is a very conspicuous ring-shaped organ lying between the two lobes of the ovary and having a diameter of 90 μ.

Vitelline Glands. These are narrow, densely granular organs

lying close to the lateral margins of the segments and staining deeply.

Uterus. No gravid uterus has been seen; the young organ consists of a central tube with irregular walls, which later on becomes sac-like. It extends in the median line almost to the anterior margin of the segment, but posteriorly it terminates near the anterior extremity of the ovarian lobes. Its posterior extremity is blind, the oviduct, as noted above, opening into it at about the level of the genital pore.

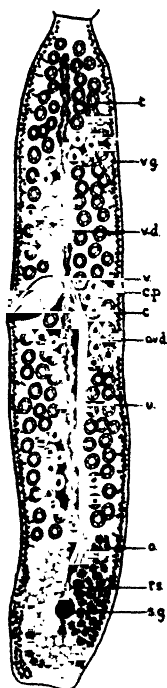


Fig. 106.—*Carpobothrium chiloscyllii.* Mature segment, × 35. (After Southwell.)

Genus V. PITHOPHORUS Southwell, 1925.

Body segmented; head consists of four bothridia, stalked or sessile; each is globular (rarely cylindrical), hollow, and open both anteriorly and posteriorly; accessory suckers absent; myzorhynchus present or absent. Genital pores marginal; vitelline glands lateral. Parasitic in elasmobranchs.

Type-species :—*Pithophorus tetraglobus* (Southwell, 1911).

Pithophorus tetraglobus (Southwell, 1911). (Figs. 107 & 108.)

Synonym:—*Orygmatobothrium tetraglobum* Southwell, 1911.

From *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Southwell.

Worms up to 9·5 cm. in length, about 1 mm. in breadth, and made up of about 70 segments. Last proglottid 3 mm. in length and 900 μ in breadth; genital pores irregularly alternate, and situated either a little in front of, or a little behind, the middle of the lateral margin of the segment.

Head. The head measures from 4 to 6 mm. in breadth and consists of four globular bothridia which are attached by a broad and rather long stalk which runs parallel to the long axis of the worm. Each bothridium measures about 1·6 mm. in length and the same in breadth; they are hollow, and open both anteriorly and posteriorly to the exterior by a wide slit. There is no myzorhynchus.

Neck. The neck is roughly cylindrical in shape, tapering posteriorly, and is 10 mm. in length.

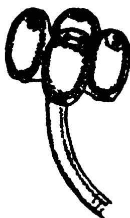


Fig. 107.—*Pithophorus tetraglobus.* Head, × 9. (After Southwell.)

Details regarding the muscular, excretory, and nervous systems are lacking.

Testes. The testes vary in number from about 130 to 170. Of these about 80 are situated aporally, whilst on the pore side about 40 testes lie anteriorly to the cirrus pouch and about 30 posteriorly to it. In full development each has a diameter of about 55 μ.

Vas deferens. The pouch lies posteriorly to the vagina and is a large, somewhat pyriform organ extending almost halfway across the segment, and measuring about 250 by 190 μ. The terminal part of the cirrus is armed with very minute spines in mature segments only, and a number of coils of the vas deferens lie within the pouch. Anteriorly to the median extremity of the sac the vas deferens forms a number of coils in the median plane. In very ripe segments the remains of the vas deferens form a conspicuous structure in the anterior

part of the median axis of the segment. Seminal vesicle apparently absent.

Ovary. When fully mature the ovary is a prominent bilobed organ extending from the posterior margin of the segment half the distance to the cirrus pouch. Each wing is shaped like an isosceles triangle, with the apex pointing anteriorly,

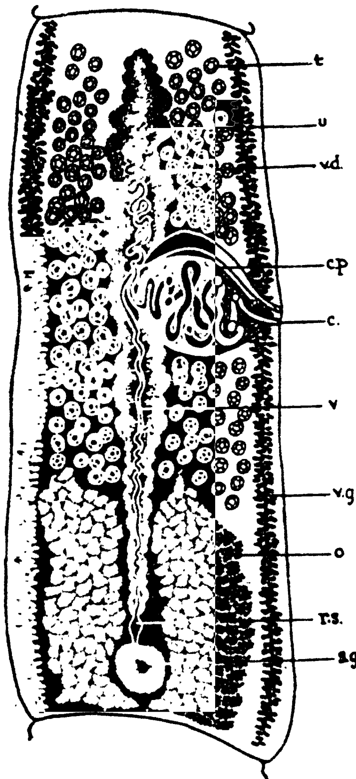


Fig. 108.—*Pithophorus tetraglobus.* Mature segment, × 46. (After Southwell.)

the bases of each triangle resting on an oblong strip of ovarian tissue. It is composed of a number of very large acini.

Vagina. From the pore the vagina runs in the median direction in front of the cirrus pouch. At the internal extremity of the latter organ it turns suddenly and runs posteriorly as a coiled tube in the middle line. Receptaculum seminis apparently absent.

Shell Gland. In mature segments this is a very prominent ring-like structure situated between the two lobes of the ovary and having a diameter of about 110 μ.

Vitelline Glands. These consist of wide bands of small acini running along each lateral margin of the segment.

Uterus. In the ripest segments the uterus consists of a narrow coiled tube running along the antero-posterior axis of the segment.

Family II. ONCHOBOTHRIIDÆ Braun, 1900.

Synonyms :—Onchobothrii Rud., 1819.
Tribe Phyllacanthiens van Ben., 1850.
Subtribe Onchobothria Diesing, 1850, *pro parte*.
Subfamily Phyllacanthina Carus, 1863.

Scolex armed with four pairs, or four groups, of simple or compound hooks. Bothridia sessile or only slightly pedunculated. Pseudoscolex present in one genus; accessory suckers present or absent. Genital pores regularly or irregularly alternate. Eggs practically unknown.

Type-genus :—*Onchobothrium* (Rudolphi, 1819).

Key to Genera.

A. Each bothridium is divided into three loculi by two transverse septa	1.
B Each bothridium is divided into two loculi by a transverse septum	2.
C. Bothridia undivided	3.
1. (*a*) Each bothridium armed with two pairs of bifurcated hooks........	ACANTHOBOTHRIUM, [p. 238.
(*b*) Each bothridium armed with two pairs of simple undivided hooks ..	CALLIOBOTHRIUM, [p. 260.
(*c*) Each bothridium armed with one pair of simple hooks, each of which may bear a tubercle or hair-like process .	ONCHOBOTHRIUM, [p. 235.
(*d*) Each bothridium armed with a pair of hooks, one of which is bifurcated and the other trifurcated	PLATYBOTHRIUM, [p. 271.
2. (*a*) Hooks bifurcated and anterior......	UNCIBILOCULARIS, [p. 265.
(*b*) Hooks not bifurcated, situated near each lateral extremity of the septa :—	[p. 288.
(1) Pseudoscolex present	THYSANOCEPHALUM,
(2) Pseudoscolex absent, hooks equal in size	SPINILOCULUS [(see Appendix).
(3) Pseudoscolex absent, hooks unequal in size................	YORKERIA, p. 285.
3. Hooks bifurcated or rose-thorn-shaped ..	PEDIBOTHRIUM, p. 276.

Genus I. ONCHOBOTHRIUM (Rudolphi, 1819), Blainville, 1828.

The bothridia are armed anteriorly with two simple hooks which may bear secondary tubercular or hair-like processes; each bothridium is divided into three loculi by two transverse septa.

Type-species :—*Onchobothrium pseudo-uncinatum* (Rudolphi, 1819), Beauchamp, 1905.

Only one species of this genus has been recorded from India, namely :—

Onchobothrium farmeri (Southwell, 1911). (Figs. 109, 110, & 111.)

Synonym :—*Calliobothrium farmeri* Southwell, 1911.

From *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

Preserved specimens measure about 6 cm. in length and have a maximum breadth of about 2·2 mm.

A large number of very shallow segments occur behind the neck, and these gradually lengthen posteriorly; the last

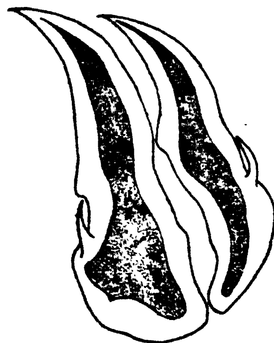


Fig. 109.—*Onchobothrium farmeri*. A pair of hooks, showing spinule, × 106. (After Southwell.)

proglottides vary in size from 1·1 to 1·2 mm. in length and 1·0 to 1·5 mm. in breadth; the genital pores are situated slightly behind the middle of the lateral margin; they are irregularly alternate and not unilateral as originally stated.

Head. The head is very large; it measures about 3·4 mm. in length and its greatest breadth is about 4 mm.; it is borne on a pedicle which is about 3 mm. in length; there are four oval bothridia, and these, although quite distinct from each other, are united by tissue from the anterior face of the head as far back as the middle areola in each bothridium.

The shape of the bothridia varies, but they measure about 3 mm. in length and 1·8 mm. in breadth; the surface of each is split up by two septa into three unequal areolæ; between the centre of the head and the most anterior areola of each bothridium there is a minute accessory sucker. Overhanging the anterior margin of the anterior areola of each bothridium there is a pair of simple, curved, hollow hooks, slightly unequal in size; they are not united at their bases, but the base of one hook appears to articulate into that of the other. The measurements of the hooks in three specimens are as follows:—Larger hook, 450, 515, and 600 μ; smaller one, 410, 455, and 540 μ. Under high-power magnifications a curved, tapering, hair-like spinule, measuring from 45 to 55 μ in length, and having a maximum diameter of about 8 μ, can be seen arising from near the base of

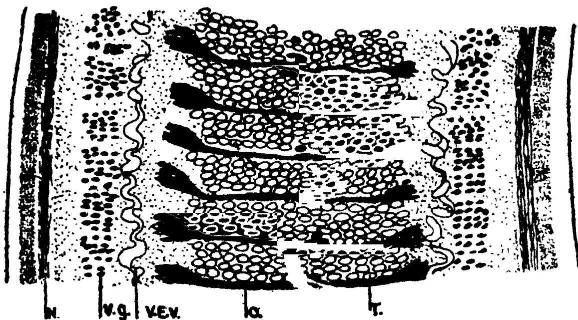


Fig. 110.—*Onchobothrium farmeri.* Horizontal section of mature segment, × 46. (After Southwell.)

the outer (lateral) margin of each hook. These spinules had not been seen when the original description of this worm was written; consequently they are not shown in the original drawings.

Neck. The neck is swollen and measures about 2 mm. in length and 1·5 mm. in breadth.

Muscular System. The longitudinal muscular system is strongly developed and consists of a single layer of about eighty large oval bundles, each of which measures about 90 by 25 μ in transverse section; they are largest on the mid-dorsal and mid-ventral surfaces, and become smaller towards each lateral margin; immediately below the cuticle (which has a thickness of about 30 μ) there is a great development of subcuticular muscle. Dorso-ventral fibres are plentiful, and they can be seen running between the bundles of longitudinal fibres;

a layer of circular muscles lies internal to the longitudinal muscles.

Testes. There are about 100 testes; when mature each one measures about 80 μ; they are situated dorsally, and lie in the central field; laterally they do not extend to the excretory vessels on either side, but they occupy practically the whole of the segment in the antero-posterior direction; they begin to atrophy when the ovary develops.

Vas deferens. The pore is situated very slightly behind the middle of the lateral margin; in mature segments the cirrus

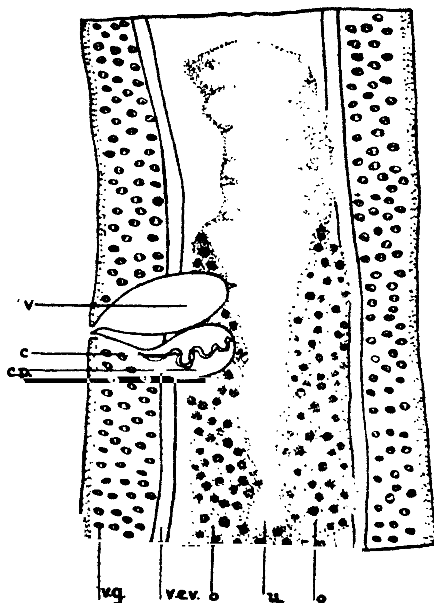


Fig. 111.—*Onchobothrium farmeri.* Horizontal section, showing developing uterus, × 46. (After Southwell.)

pouch is conspicuous, and extends internally a little median to the excretory vessels; it measures about 450 by 170 μ and lies posteriorly to the vagina between the dorsal and ventral excretory vessels. The cirrus is very muscular but not spiny; part of the vas deferens lies coiled within the cirrus pouch; after leaving the latter organ its course could not be traced. No seminal vesicle was seen.

Ovary. This lies at the posterior extremity of the segment, and its appearance varies very considerably as it becomes

mature; at first it consists of a few acini arranged in a fan-shaped manner on each side close to the excretory vessels, these being connected by a delicate transverse bridge of ovarian tissue. When fully mature the acini are disposed along three sides of a square, the lateral limbs and the posterior part, each measuring about 800 μ; it is composed of slightly club-shaped follicles having a length of about 70 μ and a diameter of about 50 μ.

The vagina is a conspicuous muscular organ.

The vitelline glands and the uterus do not differ from those of the type-species. Eggs unknown.

Genus II. **ACANTHOBOTHRIUM** van Ben., 1850.

The four bothridia are each armed with two bifurcated hooks; each bothridium is divided into three loculi by two transverse septa.

Type-species :—*Acanthobothrium coronatum* (Rudolphi, 1819), van Ben., 1850.

Key to Species.

1. The prongs of each hook are equal in length	2.
Outer prong of each hook shorter than inner prong	3.
2. Hooks about 230 μ in length, each bothridium with a single accessory sucker	*A. coronatum*, p. 238.
Hooks 140 to 170 μ in length, each bothridium with three accessory suckers	*A. ijimai*, p. 252.
3. Worms containing more than 200 segments	4.
Worms containing less than 30 segments	*A. dujardini*, p. 247.
4. Total length of hooks about 400 μ	*A. macracanthum*, p. 256.
Total length of hooks about 200 μ	*A. herdmani*, p. 250.
Total length of hooks about 100 μ	*A. uncinatum*, p. 243.

(1) **Acanthobothrium coronatum** (Rudolphi, 1819), van Ben., 1850. (Figs. 112, 113, 114, & 115.)

Synonyms :—*Tænia corollata* Abild., 1793.
Tænia rajæ-batis Rud., 1810.
Bothriocephalus coronatus Rud., 1819.
Bothriocephalus bifurcatus Leuckart, 1819.
Onchobothrium coronatum (Rud., 1819), Blainville, 1828.
Onchobothrium coronatum Molin, 1858.
Calliobothrium coronatum (Rud., 1819), Diesing, 1863.
Calliobothrium coronatum Zschokke, 1887.
Calliobothrium corollatum Monticelli, 1887.
Prosthecobothrium urogymni Hornell, 1912.
Onchobothrium tortum Linton, 1917.
Tænia dysbiotos MacCallum, 1921.

From (1) *Dasybatus kuhli* and *Urogymnus asperrimus*, Pearl Banks, Ceylon. Pearson; Hornell; Southwell. (2) *Carcharias* sp., off Negapatam, S. India. Pearson.

The synonymy of this species is somewhat complicated. Zschokke states that Abildgaard in 1793 gave a brief description of this worm, which he called *Tænia corollata*, and that Rudolphi, in error, confused it with a *Rhynchobothrium* which he named *Bothriocephalus corollatus* (Rud. Ent. ii. pt. 2, 1810, p. 63). Rudolphi in 1810 described a worm which he named *T. rajæ-batis*; in 1819 he described the same species under the name *Bothriocephalus coronatus*, and both these parasites are apparently the same as that described by Abildgaard under the name *T. corollata*. Leuckart studied Rudolphi's *T. rajæ-batis* and named it *B. bifurcatus*. Diesing referred Rudolphi's species *coronatus* to the genus *Onchobothrium*, and later (1863) placed it in the genus *Calliobothrium*. Siebold stated that

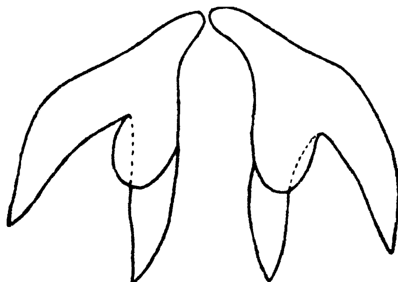


Fig. 112.—*Acanthobothrium coronatum*. A pair of hooks, × 160. (After Southwell.)

B. coronatus Rud. is the adult form of *Scolex polymorphus*, and that *B. uncinatus* is an intermediate form. Van Beneden referred Rudolphi's species *coronatum* to the genus *Acanthobothrium*.

Van Beneden's specimen had the following dimensions:—Length of whole worm, 5 to 10 cm. Length of hooks. 150 μ; length of fork of hook, 80 μ; length of ripe segments, 5 mm.; breadth of same, 3 mm.; length of penis, 500 μ; eggs, 30 μ. He (van Beneden) figures a pair of bifurcated hooks at the apex of each bothridium, each of the latter bearing an accessory sucker.

Dujardin describes *B. coronatus* Rud. as being 5 to 33 cm. in length. No accessory suckers are indicated in his figure, nor are the bothridia shown subdivided.

Zschokke's specimen measured 6 to 12 cm. in length. He does not figure the head, but states that the bothridia are subdivided into three loculi, each bothridium being surmounted

by an accessory sucker and a pair of bifid hooks; the size of the latter is not given.

Beauchamp's (1905) specimen measured 13 to 14 cm. in length. He gives no figure, but states that the bothridia are subdivided into three loculi, each one being surmounted by an accessory sucker; there are a pair of bifid hooks to each bothridium, and at the junction of the forks of each hook there is a small knob or tubercle.

Yoshida's specimens (1917) measured about 20 cm. in length and had a single accessory sucker in front of each bothridium; the hooks measured from 180 to 190 μ in length, the inner prong being a little shorter than the outer.

In our specimens the largest complete worm measured about 8 cm. in length, and the greatest breadth was about 2 mm. The total number of segments (counted under the microscope)

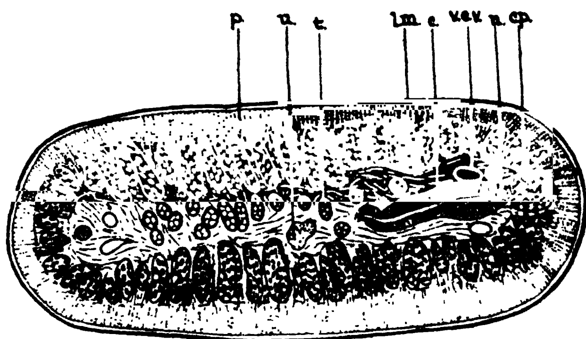


Fig. 113.—*Acanthobothrium coronatum.* Transverse section of mature segment, × 75. (After Southwell.)

was about 270; the posterior ones are much longer than broad. The genital pores are irregularly alternate and situated slightly in front of the middle of the lateral margin; the opening of the uterus on the ventral surface could be clearly seen in many segments.

Head. The head varies in length from 600 to 825 μ and has a breadth of from 680 to about 775 μ; the four bothridia are each divided into three loculi by two septa, the anterior loculus being the largest and the posterior the smallest. Each is surmounted by a single accessory sucker having a diameter of about 80 μ; between the accessory sucker and the anterior loculus of each bothridium there is a pair of bifurcated hooks having approximately the following measurements:—Total length, 230 μ; length of handle to bifurcation, 108 μ; of inner prong, 134 μ; of outer prong, 130 μ. In Zschokke's

specimens the hooks had the following dimensions :—Total length, 230 μ ; handle to bifurcation, 108 μ ; inner prong, 140 μ ; outer prong, 130 μ. Beauchamp gives the total length of the hook as 160 μ and of each fork as 100 μ.

Neck. This measures about 6 mm. in length and has a breadth of about 700 μ ; it is very muscular.

Muscular System. The longitudinal muscles are very strongly developed, especially the internal layer ; posteriorly the inner bundles decrease in size and become separated from each other. The circular fibres are well defined and situated between the outer and inner longitudinal fibres.

Excretory System. There is a pair of well-developed longitudinal vessels on each side, the ventral vessel being slightly

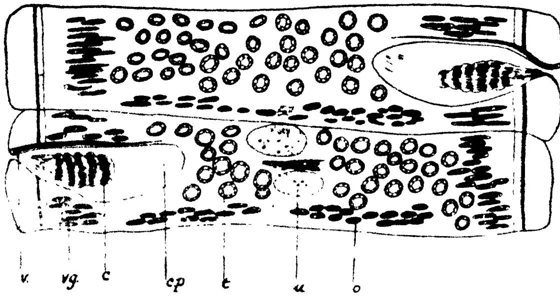


Fig. 114. *Acanthobothrium coronatum.* Almost mature segments. × 56. (After Southwell.)

the larger of the two. The vagina and cirrus pouch run between them.

Nervous System. There is a single nerve on each side situated laterally to the excretory vessels ; it is quite prominent.

The *Genital Organs* agree closely with the description given by Zschokke. The testes varied in number from about 80 to 120, and there are always more testes on the aporal side than on the pore side. The cirrus pouch is pyriform and extends almost one-fourth the distance across the segment ; a few coils of the vas deferens lie within it. Outside the pouch the vas deferens runs anteriorly near the middle line in a number of irregular coils.

The vagina has its terminal portion (near the pore) dilated almost to the size of the cirrus pouch ; the oviduct is long and opens into the uterus at a point opposite to the genital pore, and the posterior extremity of the uterus is blind. The uterine pore opens to the ventral surface.

Prosthecobothrium urogymni Hornell, 1912.

The above species appears to be identical with *A. coronatum.*

Hornell's description is as follows :—" Long, slender cestode. Head elongated, twice as long as broad, armed with four large, sessile, elongated and regularly disposed bothridia—each lanceolate and trilocular, with mobile edges and posterior tip ; anterior extremity of each bothrium tumid, armed with a pair of double dark-brown chitinous hooks. Prongs of each hook slender, equal, curved in two planes, the tips projecting beyond the anterior margin of the proximal loculus.

" Neck very long and slender ; proglottides very numerous, lateral margins slightly curved, posterior slightly overlapping,

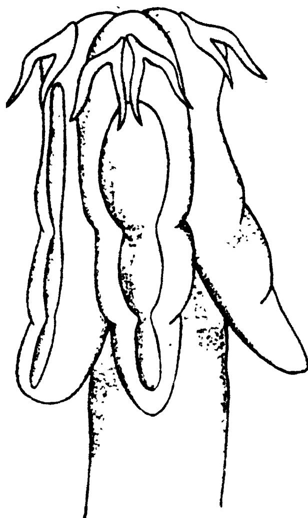


Fig. 115.—*Acanthobothrium coronatum.* Head, × 32. (After Hornell.)

usually twice as broad as long, except for a few of the most posterior. Length when alive up to 25 cm. Breadth of head under 1 mm., of typical proglottides 0·75 to 0·9 mm."

Hornell states that accessory suckers are absent ; the size of the hooks is not given, and no mention is made of the genital organs.

The head and hooks, and also the size of the worm, resemble in a remarkable degree those of *A. coronatum* (Rud., 1819) ; in fact, the only point in which Hornell's species appears to differ from *A. coronatum* is the absence of accessory suckers.

In this connection it is important to note that nearly all investigators working on the Onchobothriidæ have experienced difficulty occasionally in finding structures admittedly present. As instances Zschokke maintains that in *Calliobothrium verticillatum* there is only one accessory sucker to each bothridium, whereas all other observers have seen three clearly. The author has sometimes found it impossible to find the accessory suckers in some specimens of *A. uncinatum* (Zschokke) and *A. coronatum* (Rud.). Johnstone had difficulty in finding the third loculus in *A. dujardini*, and such instances could be multiplied. In view of these facts, and of the otherwise close resemblance of the worm to *A. coronatum*, it appears probable that Hornell's species is identical with *A. coronatum* (Rud.). Noting that Johnstone saw a third loculus in the bothridium of *A. dujardini*, Hornell proposed a modification of Diesing's genus *Prosthecobothrium* in order to accommodate his (Hornell's) specimen, and he accordingly re-defined it as follows:—"Scolex with four elongated sessile bothria divided by transverse costæ into three loculi; no accessory suckers on the anterior margins of the bothridia; a pair of double hooks on the anterior margin of each bothrium." It is clear that this emendation cannot be accepted, first because Hornell's species is apparently identical with *A. coronatum*, and, secondly, because a form actually exists in which the bothridia are divided into two areolæ.

The presence of a uterine pore, or pores, situated ventrally has been noted in the following species included in the family Onchobothriidæ, viz., *Calliobothrium verticillatum*, *Calliobothrium leuckarti*, *Calliobothrium convolutum*, *Onchobothrium nodosum*, *Acanthobothrium coronatum*, *Acanthobothrium uncinatum* (Zschokke).

(2) **Acanthobothrium uncinatum** (Rud. 1819) van Ben., 1850. (Figs. 116 & 117.)

Synonym:—*Onchobothrium uncinatum* (Rud. 1819) Blainville, 1828.

From *Dasybatus kuhli* and *D. walga*, Pearl Banks, Ceylon. Southwell.

The worms vary in length from about 3 to 5 cm.; one, which had obviously died in an extended condition, measured 8 cm.; the greatest breadth is about 1·7 mm.

Each consists of about 250 segments. The most anterior segments have a length of 30 μ; the last measure about 460 μ in length and 830 μ in breadth, but in all probability larger ones occur. The genital pores are irregularly alternate, and are situated slightly behind the middle of the lateral margin.

Head. The head is almost square and measures about 650 μ. The four bothridia are as long as the head and have a breadth of about 320 μ. Each is divided by two costæ into three loculi, the anterior loculus being the largest and the posterior one the smallest. In front of each bothridium there is a small accessory sucker having a diameter of from 30 to 40 μ, but these are sometimes difficult to see, although a membranous flap is clearly visible. Between the anterior loculus and the accessory sucker of each bothridium there is a pair of bifid hooks, the outer prong of each hook being much smaller than the inner prong. The "handle" of each hook lies embedded in a peculiar matrix or base. The measurements of the hooks are as follows :—Total length, 90 to 100 μ ; handle to bifurcation, 32 to 40 μ ; inner prong, 55 to 64 μ ; outer prong, 36 to 44 μ.

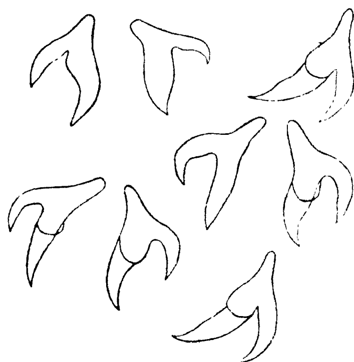


Fig. 116.—*Acanthobothrium uncinatum.* Hooks showing variations in shape, × 166. (After Southwell.)

Neck. The neck measures about 3 to 6 mm. in length ; its posterior limit is difficult to fix owing to the fact that the anterior segments are ill defined. It is somewhat triangular in shape, the anterior part having a diameter of about 700 μ and the posterior 200 μ.

Muscular System. This is very poorly developed ; the longitudinal muscles consist of a number of very small, scattered bundles which in transverse section are seen to be distributed about in the cortex. The majority of these bundles have a diameter of about 10 to 12 μ, but many smaller ones occur, and also a very few larger, having a diameter of about 25 μ, were also seen. Dorso-ventral and circular fibres were very scanty, and could only be seen here and there under a high magnification.

Testes. There are from 50 to 60 testes; when fully mature, each has a diameter of about 45 μ. In segments mounted entire they appear to occupy the whole of the medullary parenchyma on each side of the embryonic uterus, which latter develops early. In cross-section the greater number lie towards the dorsal surface, but they extend ventrally almost to the margin of the medullary parenchyma.

Vas deferens. The cirrus pouch, which passes between the two excretory vessels, lies posteriorly to the vagina, and varies a little in size and shape. It measures about 240 μ in length and 100 μ in breadth. The cirrus is very prominent both in stained and unstained specimens, and is densely covered with fine hairs or spinules. A number of coils of the vas deferens can be seen median to the cirrus within the pouch. A seminal vesicle appears to be absent.

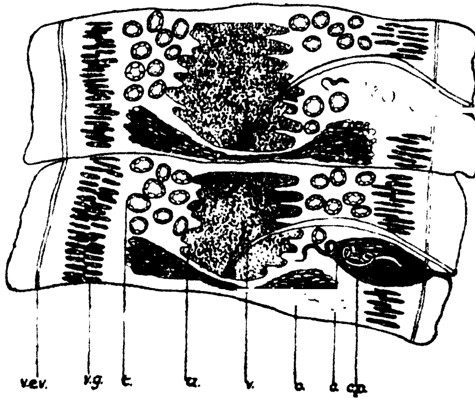


Fig. 117.—*Acanthobothrium uncinatum.* Nearly gravid segments, × 56. (After Southwell.)

Ovary. As in type-species.

Vagina. As in *A. coronatum*, except that the terminal extremity is not strikingly dilated; it is a somewhat wide tube having a diameter varying between 21 and 36 μ; receptaculum seminis apparently absent.

Vitelline Glands. As in type-species.

Uterus. No gravid uterus was present, but in the most mature segments the organ was seen as a somewhat wide, sinuous tube arising midway between the two wings of the ovary and running anteriorly; eggs are unknown.

Rudolphi's original description of this worm was as follows:—

"Bothridia each possessing two ridges (costæ); in front there

is a bifid hooklet, neck very short ; proximal segments rugose, succeeding ones varying, some being almost square."

All observers since Rudolphi, except Zschokke (1888) and Beauchamp (1905), referred to the species *uncinatum* worms which had a long neck, a single accessory sucker to each bothridium, and a pair of simple (not bifurcated) hooks. Leuckart believed that *Bothriocephalus uncinatum* Rud. was the young form of *B. coronatus*, but adduced no proof, and Siebold shared the same opinion. Dujardin believed it to be a distinct species ; he gives a short description of the worm, and a poor figure of the head. Blanchard referred it to the genus *Acanthobothrium*, but did not deal with the anatomy. Diesing placed it in the genus *Onchobothrium* (as a *sp. inquirenda*) along with *verticillatum* and *coronatum*. Van Beneden gave a description of it, and he also figured the worm, rightly concluding that *Onchobothrium uncinatum* is very different from *O. coronatum*.

Olsson (1867) mentions the worm but gives no details, and his figures are poor. Diesing in 1863 divided the Tetrabothriidæ into two groups, viz. :—(1) Those without accessory suckers, but with each bothridium divided into three loculi : this group contained the genus *Onchobothrium* only. (2) Those with accessory suckers and with each bothridium divided into three loculi ; this included *Calliobothrium*. The species *uncinatum* was referred by him to this genus.

Zschokke in 1888 pointed out the fact that Rudolphi's species *uncinatum* had bifid hooks and a short neck, whereas the *uncinatum* of all subsequent observers had simple hooks and a long neck. He accordingly described another worm under the name *uncinatum*, which had bifid hooks and a short neck. He also pointed out that (1) the anatomy of the forms included in the genera *Onchobothrium* and *Calliobothrium* is similar, and (2) that it is therefore undesirable to retain the genus *Onchobothrium*. It is clearly impossible to say whether Zschokke's species is the same as that briefly described by Rudolphi : Zschokke, however, is correct in his remarks, and his description must be accepted, but as this species possesses bifid hooks it must be placed in the genus *Acanthobothrium* van Ben.

Beauchamp (1905) proposed the name *O. pseudo-uncinatum* for the species possessing one pair of simple hooks to each bothridium, and this, too, must be accepted.

A comparison of the measurements of our worm and Zschokke's is given below.

There can be no doubt that the Ceylon specimens are identical with *A. uncinatum* (Zschokke). The only other species having bifurcated hooks, the outer prong of which is much shorter than the inner, are :—(a) *A. paulum* Linton,

1890: this species has only about thirty segments, and measures from 5 mm. to 1·9 cm. in length; the hooks have a total length varying between 140 to 200 μ in different specimens, the largest prong being 100 to 140 μ. (b) *A. brevissime* Linton, 1909: this worm measures from 1 to 2 mm. and has about 10 segments only; the hook has a total length of about 120 μ; the outer prong measures about 66 to 72 μ and the inner 86 to 90 μ.

	Zschokke's *Onchobothrium uncinatum*.	Ceylon specimens.
Length of worm	20 mm. to 4·5 cm.	3 to 5 cm. One 8 cm.
Breadth of worm	1·2 mm.	1·7 mm.
Length of neck	5 mm. to 1 cm.	3 to 6 mm.
Length of head	700 μ	650 μ
Breadth of head	600 μ	650 μ
Length of bothridia	600 μ	650 μ
Breadth of bothridia	270 μ	320 μ
Length of hook	110 to 126 μ.	90 to 100 μ.
Handle of hook	23 μ	20 μ
Handle to bifurcation	46	40 μ
Outer prong	38 to 44 μ.	36 to 44 μ.
Inner prong	72 μ	55 to 64 μ.
Number of segments	150 to 200	250
Number of testes	50 to 66	50 to 60

(3) **Acanthobothrium dujardini** van Ben., 1850. (Figs. 118 & 119.)

Synonyms:—*Onchobothrium* (*Acanthobothrium*) *papilligerum* Diesing, 1854.
Prosthecobothrium dujardinii Diesing, 1863.
Acanthobothrium coronatum vars. of Pintner and Niemiec.
Acanthobothrium brevissime Linton, 1908.
Prosthecobothrium dujardinii (van Ben.) Johnstone, 1910.
Acanthobothrium semnovesiculum Verma, 1928.

From (1) *Dasybatus walga*, Ennur, Madras, India. Pearson. (2) *D. sephen*, Rivers Ganges and Jumna, Allahabad, India. Verma.

The worms vary in length from 1 to 2 mm. and the maximum breadth from 166 to 220 μ. The strobila contains from eight to twelve segments, the last measuring 480 μ in length and 140 to 170 μ in breadth: the genital pores are irregularly alternate and situated a little anteriorly to the

centre of the lateral margin of the segment. Calcareous corpuscles were very abundant.

Head. The four bothridia vary a little in size and shape, measuring about 220 μ in length and 75 μ in breadth. Their surfaces are divided by two costæ into three loculi, of which the anterior is the largest and the posterior the smallest. Sometimes it is difficult to see more than two loculi. Anterior to each bothridium there is a triangular pad bearing a single accessory sucker. Between the anterior loculus and accessory sucker of each bothridium there is a pair of bifurcated hooks, the outer prong of each hook being shorter than the inner

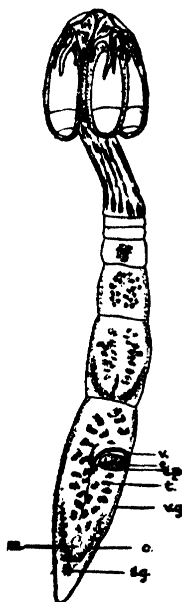


Fig. 118.—*Acanthobothrium dujardini.* Entire worm, × 56. (After Southwell.)

one. The dimensions of the hooks are as follows :—Total length, 115 to 123 μ ; handle to bifurcation, 33 to 36 μ ; outer prong, 66 to 72 μ ; inner prong, 86 to 90 μ. The inner prong bears a small tubercle near its origin.

Neck. The neck is very short, measuring only about 200 μ in length. It is armed with innumerable spines. Bands of stout longitudinal muscles could be clearly seen running to the head.

Details of the muscular, excretory, and nervous systems are not known.

Testes. There are about twenty oval testes, having their long diameters parallel to the transverse axis of the segment; they are arranged on each side of the median longitudinal line. They vary in size within fairly wide limits, the anterior and posterior testes being smaller than the rest.

Vas deferens. The cirrus pouch is large and conspicuous, extending in the median direction to the centre of the segment. It measures about 75 μ in length and 40 μ in breadth. The cirrus is thickly beset with small spines; a few coils of the vas deferens lie within the pouch, but its course outside the latter organ is very short. No seminal vesicle has been observed.

Ovary. This is an U-shaped organ extending on the pore

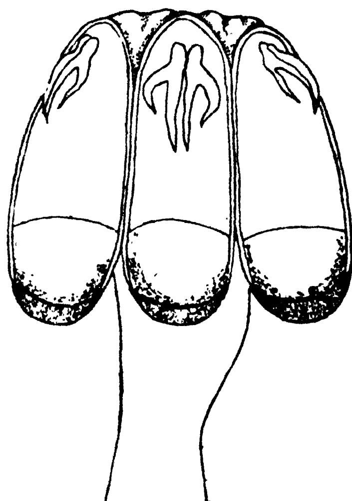


Fig. 119.—*Acanthobothrium dujardini.* Head, × 216. (After Southwell.)

side to the cirrus pouch, the aporal half being only about 30 μ longer. Both arms have a diameter of about 20 μ.

Vagina. The vagina runs anteriorly to the cirrus pouch, and is a thick-walled tube having an even diameter of about 15 μ. From the pore it extends in the median direction; curving round the median extremity of the cirrus pouch, it pursues a slightly sinuous course directly backwards to the ovaries. A receptaculum seminis is apparently absent.

Vitelline Glands. These consist of a single row of oval acini extending the whole length of the segment immediately internal to the subcuticular muscles.

The uterus has not been described and the eggs are unknown.

(4) **Acanthobothrium herdmani** Southwell, 1912. (Figs. 120, 121, & 122.)

From *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

The worm consists of over two hundred segments and measures about 6·3 cm. in length and 2 mm. in breadth; the genital pores are irregularly alternate and situated near the middle of the lateral margin.

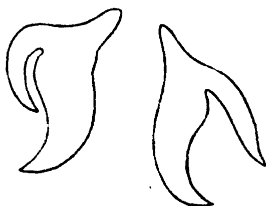


Fig. 120.—*Acanthobothrium herdmani*. Hooks, × 250. (After Southwell.)

Head. The head measures about 1·3 mm. in length and 1·6 mm. in breadth. The four bothridia have their surfaces split up into three loculi by two septa, the anterior loculus being the largest and the posterior the smallest; each bothridium is surmounted by a single accessory sucker. Between the

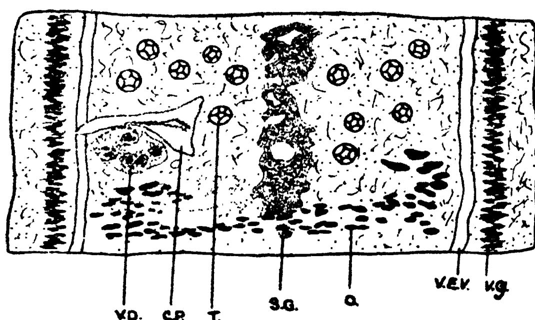


Fig. 121.—*Acanthobothrium herdmani*. Horizontal section of mature segment. × 46. (After Southwell.)

anterior loculus and accessory sucker of each bothridium there is a pair of bifid hooks, the outer prong of each hook being shorter than the inner prong. In this respect *A. herdmani* bears a slight resemblance to *A. uncinatum* (Zschokke), but the hooks of the two species differ widely in size. In

A. herdmani they have the following dimensions:—Total length, 200 μ; handle to bifurcation, 97 μ; outer prong, 90 μ to 96 μ; inner prong, 126 μ.

Neck. The neck varies in length from about 2 to 5 mm. and merges imperceptibly into the strobila.

Muscular System. A well-developed layer of subcuticular fibres is situated immediately beneath the cuticle. The dorso-ventral fibres are prominent; the principal muscles consist of a single layer of large longitudinal bundles, internal to which there are a few circular fibres, but the latter are scanty.

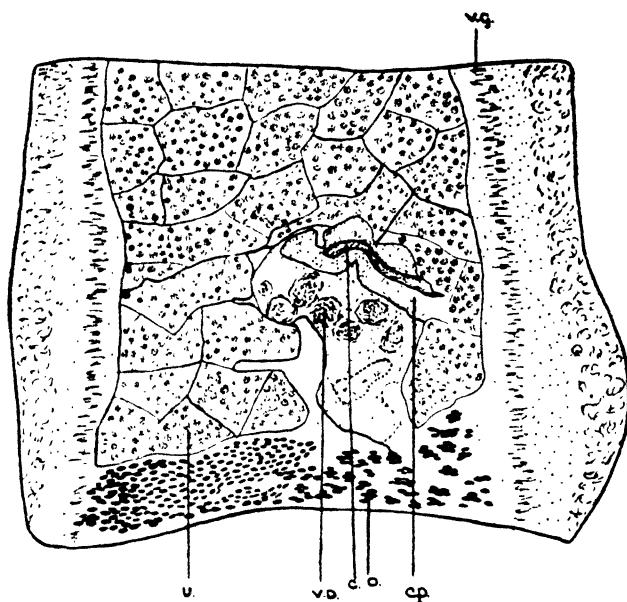


Fig. 122. *Acanthobothrium herdmani.* Horizontal section of gravid segment, × 75. (After Southwell.)

Excretory and Nervous Systems. As in *A. coronatum.*

Testes. There are about 100 testes, each having a diameter of about 75 μ: at first they are situated in two lateral groups. When mature, they occupy the whole of the dorsal surface. On the pore side about sixteen testes lie posteriorly to the cirrus pouch.

Vas deferens. The cirrus pouch is large and situated behind the vagina; the cirrus is armed with very numerous small spines, and a number of coils of the vas deferens lie within the pouch. Outside this organ the vas deferens extends to the middle of the segment, and then turns forwards.

Ovary. The ovary is a bilobed organ situated posteriorly, each lateral extremity being extended fan-wise. It is composed of oval acini, the largest of which measures about 75 μ in length.

Vagina and Vitelline Glands. As in type-species.

Shell Gland. This is a small granular organ situated behind the centre of the ovary.

Uterus. The uterus arises as a solid mass of cells running from the ovary to the anterior extremity of the segment. Later on it becomes hollow and, as it develops, the walls become lobulated. Eventually it fills the entire segment, the cavity being split up into compartments by ingrowths of the uterine wall.

(5) **Acanthobothrium ijimai** Yoshida, 1917. (Figs. 123, 124, 125, & 126.)

Synonyms:—*Acanthobothrium coronatum* Johnstone, 1906, not Rudolphi, 1819.
Acanthobothrium coronatum Linton, 1901, not Rudolphi, 1819.
Tænia incognita MacCallum, 1921.

From *Narcine timlei*, Negapatam, S. India, and *Chiloscyllium* sp., Pearl Banks, Ceylon. Southwell.

The worms vary in length from about 2 to 5 cm., and they have a maximum diameter of approximately 1 mm.

The total number of segments, counted under a microscope, varies from about 80 to 100. The most anterior ones have a length of about 18 μ and a breadth of about 830 μ. The largest has a length of 1·5 mm. and a breadth of 900 μ. No gravid segments have been seen; the edges of the proglottides are straight, not convex. The genital pores are irregularly alternate and are situated distinctly behind the centre of the lateral margin.

Head. The head varies from about 1 to 1·2 mm. in length and from 900 μ to 1·15 mm. in width. The four bothridia have a length of from 700 to 760 μ and a breadth of 450 to 530 μ, but vary considerably. They are each divided into three loculi, of which the anterior one is the largest and the posterior the smallest. Overhanging each anterior loculus is a pair of bifurcated, equal-pronged hooks having the following dimensions:—Total length, 133 to 144 μ; handle to posterior point of bifurcation, 54 to 61 μ; inner prong, 80 to 83 μ; outer prong, 80 to 92 μ. These hooks vary in shape a little, and the internal prong of each bears a somewhat large tubercle. In front of each pair of hooks there are three large accessory suckers, each very muscular and situated so close together that their walls are in contact. Their diameter varies from about 120 to 180 μ.

In some specimens the hooks have the following measurements :—Total length, 170 μ ; handle to bifurcation, 75 μ ; length of inner prong, 95 μ ; length of outer prong, 72 (curved) to 95 μ.

Fig. 123.

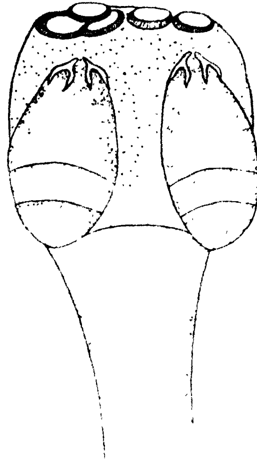
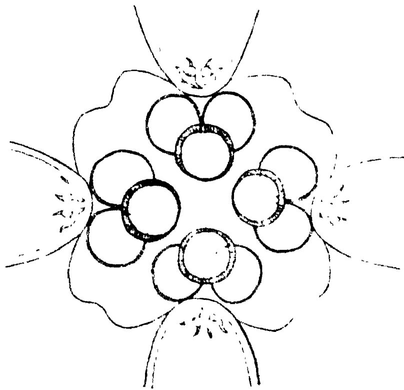


Fig. 124.



Acanthobothrium ijimai.

Fig. 123.- Head, × 35. (After Southwell.)
Fig. 124.- Head viewed *en face*, showing the hooks, accessory suckers, and anterior extremities of the bothridia. × 34. (After Southwell.)

Neck. The neck varies in length from about 700 μ to about 1·5 mm. ; in the species described by Johnstone the neck measured 3·5 mm. Where it joins the head it is wide

and has a diameter of from 900 μ to 1 mm. It narrows a little posteriorly.

Muscular System. This is very poorly developed, and consists of a few exceedingly small longitudinal fibres. In the neck, however, about eight large bundles can be seen running to the head.

Excretory System. This also is very feebly developed; there are two very small vessels on each side which frequently cannot be seen at all. The dorsal vessel is the larger of the two, and the vagina and cirrus pouch run between them.

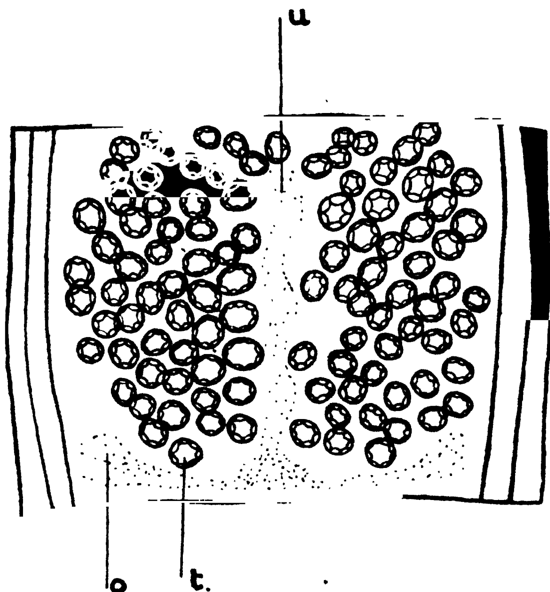


Fig. 125.—*Acanthobothrium ijimai.* Male mature segment, × 69. (After Southwell.)

Testes. The testes vary in number from about 90 to 110; in unripe segments they are oval and are distributed in transverse rows in the lateral fields. When mature they are still oval in shape, and have a maximum length of about 180 μ and a breadth of about 55 μ; in total mounts they appear to occupy the whole of the segment, and their arrangement in transverse rows is lost.

Vas deferens. The cirrus pouch is a large and conspicuous organ varying a little in size and shape; it is usually oval, and measures about 380 μ in length and 230 μ in breadth. It lies posteriorly to the cirrus and runs between the two excretory

vessels. The cirrus is also a prominent organ, and is densely armed with very minute spines. A few coils of the vas deferens lie within the pouch, but outside the pouch it can only be traced a very short distance. A seminal vesicle appears to be absent.

Ovary. The ovary does not begin to appear until the testes are fully developed. It is then an U-shaped organ situated along the posterior and postero-lateral margins. The two limbs are not of equal lengths, for on the pore side it only extends to the posterior margin of the cirrus pouch, whilst on the aporal side it reaches more anteriorly. The poral limb measures about 530 μ antero-posteriorly, while the

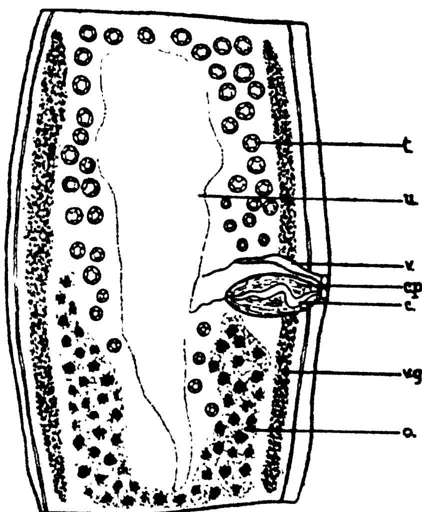


Fig. 126.—*Acanthobothrium ijimai.* Mature segment, × 46. (After Southwell.)

aporal one is about 750 μ. Both have a diameter of from 170 to 220 μ.

Vagina and Vitelline Glands. As in type-species.

Uterus. No trace of the uterus can be seen until the ovaries are fairly well developed. In the most mature segment (no gravid segments have been seen) it consists of a tubular cavity with irregular lateral outpocketings running along the middle line from the posterior to the anterior extremity; eggs unknown.

The only species of the genus *Acanthobothrium* which possesses a triple accessory sucker to each bothridium is

A. ijimai. Yoshida described the species from three specimens in which the genitalia had not developed ; a comparison of the genital organs is therefore impossible.

It will be noted that the size of the bothridia and neck vary considerably, but not to a greater extent than the author has frequently observed in preserved specimens of other species. Yoshida states that of the three accessory suckers one is twice as long as the other two. In Johnstone's specimens the suckers varied a little in size, but no constancy was observed. In Yoshida's specimens the hooks had a maximum length of 110 μ, whilst in Johnstone's specimens they measured about 144 μ. It will be noted, however, that Yoshida's types were immature. There can, I think, be no doubt that Johnstone's worms are identical with Yoshida's type *A. ijimai.*

Linton's specimens measured about 5 cm. in length ; each bothridium bore three accessory suckers ; the hooks had the following dimensions :—Total length, 170 μ ; handle to bifurcation, 66 μ : outer prong, 98 μ ; inner prong, 94 to 104 μ ; length of head, 825 to 900 μ ; breadth of head, 750 to 825 μ. The neck measured about 5 mm. in length, and the anatomical characters of Linton's and Johnstone's specimens are identical. Linton ('Parasites of Fishes of the Woods Hole Region') figures the species as possessing three accessory suckers to each bothridium.

(6) **Acanthobothrium macracanthum** Southwell, 1925. (Figs. 127 & 128.)

From *Urogymnus* sp. (? *asperrimus*), Pearl Banks, Ceylon. Hornell.

The worm measures 21 cm. in length and its maximum breadth is 700 μ ; it is composed of several hundred segments ; about a hundred of the anterior ones are exceedingly shallow, and many of them can only be seen under a high-power magnification. The last proglottid measures 900 μ in length and 340 μ in breadth.

The genital pores are irregularly alternate and situated laterally ; their position varies considerably ; occasionally they are placed at the middle, and even very slightly posteriorly to the middle of the lateral margin of the segment. Usually, however, they lie a little in front of the centre, but occasionally they are actually in the anterior third of the segment.

Head. This measures 1·8 mm. in length and its breadth is 1 mm. ; each bothridium is 1·5 mm. in length and 450 μ in breadth ; the anterior loculus attains 650 μ in length and the middle and posterior ones each 300 μ in length. In front of each bothridium there is a pair of very large bifurcated

hooks, the inner prong of which is longer than the outer prong and bears a tubercle ; the size of the hook is as follows :—Total length, 490 μ ; handle to bifurcation, 220 μ ; inner prong, 300 μ ; outer prong, 235 to 245 μ ; in front of each pair of hooks there is a single accessory sucker having a diameter of about 75 μ.

Neck. The neck measures about 1 mm.

Details of the muscular, excretory, and nervous systems are not known, as only one specimen was available, but in the neck there are four stout muscular bands, each having a diameter of 75 μ ; a single band runs to each bothridium.

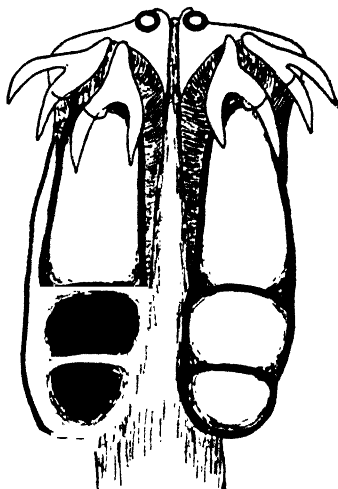


Fig. 127.—*Acanthobothrium macracanthum* Head, × 35. (After Southwell.)

Testes. The testes appear about 3 mm. behind the head ; they vary in number from about 42 to 53 ; aporally there are from about 25 to 32 ; on the pore side there are from 10 to 15 anteriorly and 7 or 8 posteriorly to the cirrus pouch. When fully developed they each have a diameter of about 55 μ, and they occupy a very large number of segments.

Vas deferens. The cirrus pouch lies behind the vagina and extends almost to the middle of the segment ; the cirrus is long and lies coiled within the pouch ; it is armed with innumerable spines. The median extremity of the pouch is occupied by a few coils of the vas deferens ; outside the sac a few loops of the vas deferens can be seen in front of the cirrus pouch near the antero-posterior axis of the segment, as in the type-species. No seminal vesicle was seen.

Ovary. The ovary appears about 4·5 cm. behind the head, and it is present in a large number of segments ; it lies quite posteriorly and is U-shaped ; the poral wing reaches forwards as far as the cirrus pouch, but the aporal one is longer, extending anteriorly beyond that level. The acini are globular, and when fully developed each has a diameter of about 34 μ ; the aporal lobe is composed of about 33 and the poral of about 29 acini. The two oviducts, one from each half of the ovary, are prominent and meet in the middle line, just in front of the posterior extremity of the ovary, to form a common oviduct.

Vagina. As in the type-species ; the poral swelling extends quite one-third the distance across the segment and appears

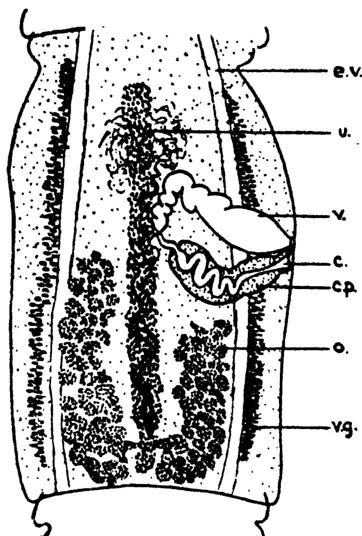


Fig. 128.—*Acanthobothrium macracanthum*. Mature segment, × 75. (After Southwell.)

to function as a receptaculum seminis ; no other dilatation was seen on the vagina, but at the median extremity of the enlargement it is thrown into a number of coils.

Shell Gland. What appears to be the shell gland consists of granular material disposed as a small globular mass round the fertilization canal ; it had a diameter of about 20 μ.

Uterus. The uterus only differs from that of the type-species in that its posterior extremity is continuous with the oviduct ; no eggs were seen.

In the table on p. 259 a comparison is made between the six different species of the genus *Acanthobothrium*.

Table showing Principal Differences between the Six Indian Species of Acanthobothrium.

	A. herdmani.	*A. uncinatum.*	*A. coronatum.*	*A. ijimai.*	*A. macracanthum.*	*A. dujardini.*
Length of worm	6·3 cm.	3 to 8 cm.	8 cm.	2 to 5 cm.	21 cm.	1 mm. to 2 cm.
Breadth of worm	2 mm.	1·7 mm.	2 mm.	1 mm.	700 μ	200 to 500 μ
Head long	1·2 mm.	650 μ	600 to 800 μ	1·2 mm.	1·8 mm.	200 μ
Head broad	1·7 mm.	650 μ	680 to 770 μ	900 μ to 1·1 mm.	1·0 mm.	110 μ
Neck	Long.	3 mm. to 6 mm.	6 mm.	700 μ to 1·5 mm. (3·5 mm. Johnst.)	1·0 mm.	200 μ ; spiny ?
Number of segments	Over 200; salient, thick.	250	270	80 to 100	Several hundred.	6 to 12
Hook, total length	200 μ	90 to 100 μ	230 μ (260 μ Linton).	133 to 170 μ	490 μ	73 to 120 μ (170 μ van Ben. ?)
Handle to bifurcation	100 μ	32 to 40 μ	108 μ	54 to 61 μ	220 μ	15 to 35 μ
Inner prong	126 μ	55 to 64 μ	134 μ	80 to 104 μ	300 μ	54 to 90 μ
Outer prong	90 μ	36 to 44 μ	130 μ	80 to 98 μ	235 to 245 μ	30 to 72 μ
Accessory suckers	1	1	1	3	1	1
Pore	Irregularly alternating, middle.	Irregularly alternating, slightly behind middle.	Irregularly alternating, front of middle.	Irregularly alternating, posterior.	Position varies, near middle; irregularly alternate.	In anterior third of segment. Irregularly alternate.
Musculature	Feebly developed.	Feebly developed.	Strongly developed.	Feebly developed.	?	?
Testes	100	50 to 60	80 to 120	90 to 110	42 to 53	20
Remarks	Worm oval in cross-section.	Base of hook 54 μ to 72 μ.	Uterine pore present.	—	—	—

Genus III. CALLIOBOTHRIUM van Ben., 1850.

The four bothridia each carry two pairs of simple (not bifurcated) curved hooks. Each bothridium is divided into three loculi by two transverse septa.

Type-species :—*Calliobothrium verticillatum* van Ben., 1850.

Key to Species.

Small worms up to 10 mm., with from ten to twenty segments........................	*eschrichtii*, p. 263
Large worms with numerous segments, the posterior margins of which are markedly laciniated.......	*verticillatum*, p. 260.

(1) **Calliobothrium verticillatum** (Rud. 1819) van Ben., 1850. (Figs. 129 & 130.)

Synonyms :—*Bothriocephalus verticillatus* Rudolphi, 1819.
Onchobothrium verticillatum Diesing, 1850.
Tetrabothrium verticillatum (Rudolphi, 1819) Wagener, 1854.

From *Carcharis* sp., Negapatam, Madras Pres., India. Pearson.

The specimens vary in length from 2 to 4·5 cm. and the greatest breadth from 500 μ to 1·5 mm. Yoshida has recorded a specimen which consisted of 580 segments and which measured 14 cm. in length and 1·1 mm. in maximum breadth. The shapes of the proglottides vary in different parts of the worm. The most anterior ones have their posterior lateral margins produced into four triangular flaps, two being dorsal and two ventral. Further back the middle of the posterior margin of the segment grows out into a rounded lobe which later on divides into two. There are then four triangular flaps on the dorsal posterior margin of each segment and four similar flaps ventrally. More posteriorly the four median flaps (two dorsal and two ventral) disappear, leaving only the four original lateral posterior flaps. These latter at this stage are large and have rounded hinder margins. The genital pores are situated in the anterior third of the segment and are irregularly alternate.

Head. This measures 1·6 mm. in length. Each bothridium is divided into three loculi, the anterior one being quite half the length of the entire bothridium ; each of the latter bears two pairs of simple hooks which measure about 90 μ in length. Johnstone gives the size of the hooks as 95 μ and Yoshida as 100 μ. There are three accessory suckers to each bothridium. Zschokke states that there is only a single accessory sucker, and he only figured one, but all other observers (Linton, Monticelli, Johnstone, Yoshida) have seen and figure three. There is no neck.

Muscular System. This is feebly developed. The longitudinal fibres are extremely small and very scanty, and can be seen, under a high-power magnification, lying immediately within the cuticle. No circular ones could be seen, but a few oblique muscles were observed running between the longitudinal fibres.

Excretory System. There are two vessels on each side, the ventral being the larger. The dorsal one lies median and a little dorsally to the ventral; the vagina and cirrus pouch both run dorsally to the two water vessels.

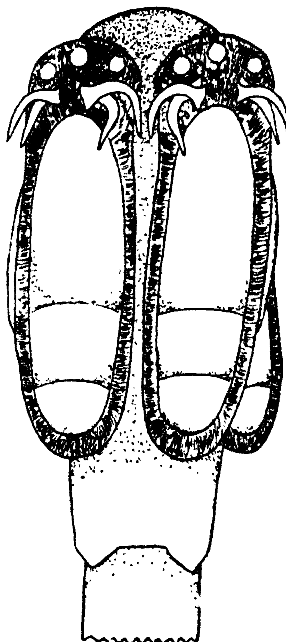


Fig. 129.—*Calliobothrium verticillatum.* Head, × 160. (After Southwell.)

Nervous System. There is a single nerve strand on each side lying laterally to the dorsal and ventral water vessels.

Testes. There are about 115 to 135 testes; at first these are situated in the two lateral fields, but when fully grown they extend and occupy the whole of the dorsal part of the segment. Each testis measures about 70 μ when mature.

Vas deferens. The cirrus pouch is comparatively small; it is pyriform (almost globular) in shape, and in full development measures about 130 μ in diameter. In the median direction it only extends to the internal edge of the vitelline

glands ; it lies dorsally to both water vessels. The terminal portion of the cirrus is enlarged and glandular, but no spines were observed. Outside the pouch the vas deferens is long and coiled and occupies a considerable portion of the anterior and median part of the segment ; it can be very clearly seen in proglottides in which the testes have degenerated and the uterus commenced to develop.

Ovary. The ovary is a large two-winged organ occupying the posterior quarter of the segment ; it is composed of rather large acini.

Vagina. The terminal portion of the vagina is glandular and

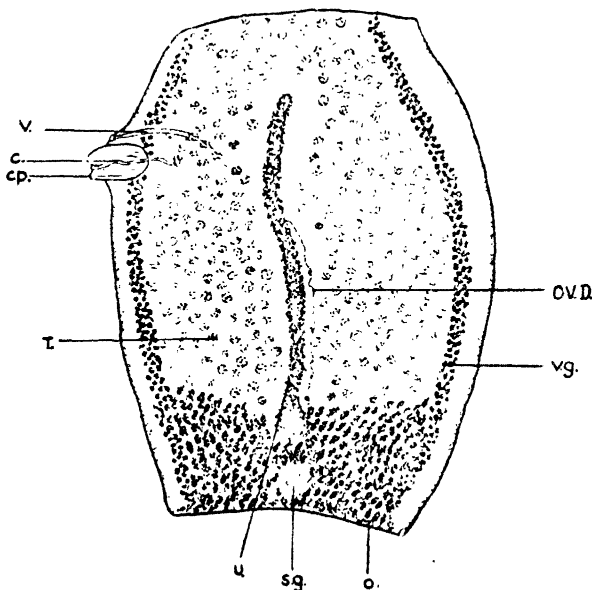


Fig. 130.—*Calliobothrium verticillatum.* Mature segment, × 212. (After Southwell.)

runs anteriorly to the cirrus pouch and dorsally to both water vessels. It crosses the median extremity of the cirrus pouch and then turns and runs backwards. In front of the ovary it dilates into a receptaculum seminis. The shell gland is large and prominent and is situated behind the ovary.

Vitelline Glands. In ripe segments these glands occupy the lateral margins ; extending the whole length of the segment, they have a breadth of about 75 μ.

Uterus. Zschokke rightly pointed out that in this species the posterior extremity of the uterus is blind, and the oviduct runs forward to a point near the genital pore, where it enters the

uterus. The rudiment of the uterus appears very early, even before the testes are to be seen. It elongates antero-posteriorly as the segment grows, and when the ovaries are fully developed the wall of the uterus becomes lobulated. At this stage it can be clearly seen that the posterior extremity is blind and not in communication with the oviduct. The latter, running forwards in an undulating course, enters the uterus, as noted above, just opposite the genital pore.

Eggs. Unknown.

This species is easy to identify on account of (1) its hooks; (2) the peculiar laciniation of the posterior margin of the segments; (3) the genital pore being in the anterior third of the segment; and (4) the anterior prolongation of the oviduct.

(2) **Calliobothrium eschrichti** (van Ben., 1850). (Figs. 131 & 132.)

Synonyms:—*Acanthobothrium eschrichtii* van Ben., 1850.
Onchobothrium elegans Diesing, 1854.

From *Dasybatus sephen*, Chilka Lake, Orissa, India. Southwell.

Van Beneden in 1850 gave the following dimensions of the worm:—Length of strobila, 4 to 5 mm.; length of hooks, 100 μ; length of segment, 8 to 9 mm. (*sic*, 0·8 to 0·9 mm. ?). He figures the worm as possessing two pairs of hooks and an accessory sucker to each bothridium, the latter being divided by two costæ into three loculi; about seven testes are shown in each segment.

Linton's largest specimen (1891) measured 14 mm. and his smallest 6 mm. He gives the following dimensions of two living specimens:—Length, 6 to 9 mm.; length of head, 900 μ; length of bothridia from hooks to posterior end, 600 to 640 μ; breadth of bothridia, 340 μ; length of hooks, 200 to 240 μ; diameter of neck, 200 to 240 μ; length of last segment, 1 mm.; breadth of last segment, 320 to 600 μ. The total number of segments in each of the above specimens was about fifteen.

This author, accepting van Beneden's statement that the last segment of van Beneden's worm measured 8 to 9 mm. in length, calls attention to the fact that in his own specimens the last segment never measured more than 1·5 mm. It is clear that the difference is due to a misprint in van Beneden's paper.

He adds the following details:—"Genital pores in the posterior third of segment; cirrus long and unarmed. Ovaries two, oblong, on either side of median line, confluent posteriorly, occupying nearly the posterior third of the length of the segment. The segmented interior of the eggs of a stellate shape; each process knobbed at its extremity.

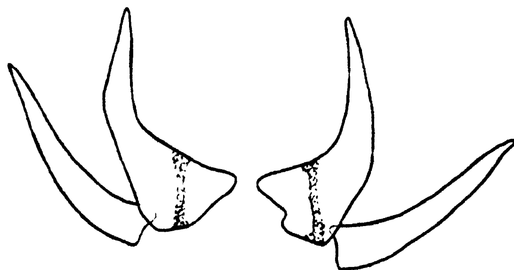
The 'ova' (eggs ?) measured from 160 to 320 μ, after being in water." He figures about fifty testes in each segment.

Yoshida's (1917) specimens measured 4 mm. in length, and

Fig. 131.



Fig. 132.





Calliobothrium eschrichti.

Fig. 131.—Head, × 75. (After Southwell.)
Fig. 132.—Hooks, × 160. (After Southwell.)

the greatest breadth was 250 μ. He does not describe the anatomy, nor does he figure the worm.

This species is easy to identify on account of its small size and the shape of the hooks.

Genus IV. UNCIBILOCULARIS Southwell, 1925.

It has been already stated that van Beneden in 1850 described the bothridia of *Acanthobothrium dujardinii* as possessing two loculi only, and that Diesing in 1863 erected the genus *Prosthecobothrium* to accommodate this species. In 1870 van Beneden re-figured his species *Acanthobothrium dujardinii*, and in this second illustration the bothridia were shown possessing three loculi. Beauchamp states that up to 1905 Olsson was the only person who had seen specimens of *Acanthobothrium dujardinii* having biloculated bothridia. Johnstone in 1910 figured a specimen of *Acanthobothrium dujardinii* having three loculi, but stated that the posterior costa and loculus were most "difficult to see."

As the number of loculi in *Acanthobothrium dujardinii* either vary, or one of them is so small that it cannot always be seen, it is obvious that the species cannot be relegated to Diesing's genus *Prosthecobothrium*. This genus accordingly becomes a *nomen nudum*. It was thus necessary to erect a new genus to accommodate a species having an armed head in which each bothridium is divided by a single septum into two loculi. The writer in 1925 proposed the name *Uncibilocularis*, with the following characters :—

Each bothridium has its surface divided into two loculi by a single septum, and is armed anteriorly with either simple or compound hooks. Accessory suckers present or absent.

Type-species :—*Uncibilocularis trygonis* (Shipley & Hornell, 1906).

Key to Species.

Hooks 140 to 170 μ in length	*U. trygonis*, p. 265.
Hooks about 500 μ in length..................	*U. mandleyi*, p. 269.

(1) **Uncibilocularis trygonis** (Shipley & Hornell, 1906). (Figs. 133, 134, & 135.)

Synonym :—*Prosthecobothrium trygonis* Shipley & Hornell, 1906.

From *Dasybatus walga* and *D. sephen*, Pearl Banks, Ceylon. Hornell.

Shipley and Hornell in 1906 described this worm as follows :—

"One specimen of this cestode was taken from the intestine of *Trygon walga* and three from *Trygon sephen*. The longest measured, when preserved, 120 mm. in length. The worm is very narrow, 0·5 mm. only in breadth, though posteriorly it broadens out to a couple of millimetres.

"The head is 1 mm. in width. It is square, something like a cushion which is indented in the centre and along the lateral

and dorso-ventral axes. The head is thus divided into four squares of equal area, and each of these squares bears at its external angle, anteriorly, a large hollow or bothridium, on the anterior edge of which lie the hooks mentioned below. Behind each is a single, round, rather small, but quite conspicuous sucker. This sucker is a simple sucker and has no sub-divisions or areolas. On its surface each of the four squares bears two hooks more or less connected at their base; each hook is forked and consists of two unequal-sized prongs; of these, that which is next the diagonal lines or lines adjoining the bases of the suckers is the larger and bears a tubercle

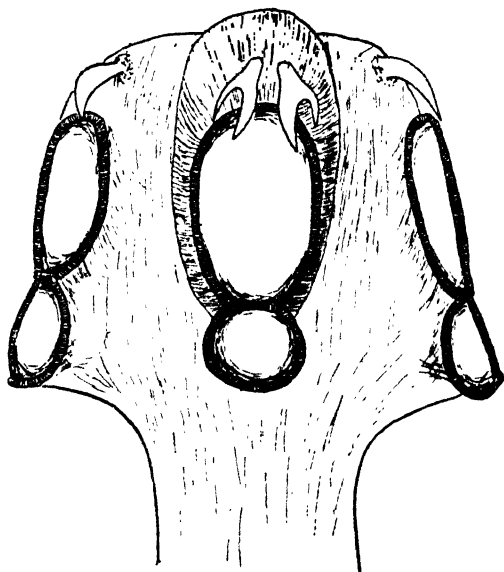


Fig. 133.—*Uncibilocularis trygonis.* Head, × 75. (After Southwell.)

at its base. The hooks are dark-brown, chitinous-looking structures.

"The neck is very long, 2 cm. or 3 cm. at least. . . The proglottides are extremely numerous; they have salient posterior angles. They always remain somewhat broader than they are long, even at the posterior end, except perhaps the very last. . ."

The hooks of this species bear a close resemblance to those of *A. herdmani* Southwell, 1912, and *A. uncinatum* (Rud., 1819), but the authors do not give the measurements. Unfortunately Shipley and Hornell's specimens appear to have been lost.

The worms measure about 6·5 cm. in length, and the greatest breadth is about 1·5 mm. They are composed of a very large number of shallow segments, which elongate slowly toward the posterior extremity. The penultimate segment in each worm was square, and the last segment measured about 600 μ in length and 450 μ in breadth. The genital pores are irregularly alternate and are situated laterally very close to the anterior corner of the proglottis.

Head. The head measures 750 μ in length and 680 μ in breadth in one strobila, and 750 μ in length and 825 μ in breadth in the other specimen. The bothridia are from 530 to 570 μ in length and 250 μ in breadth. They are divided into two very clear loculi by a single septum, each loculus being almost circular. The anterior one has a

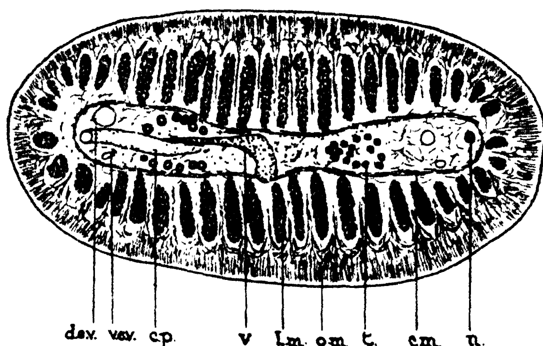


Fig. 134.—*Uncibilocularis trygonis.* Transverse section of mature segment, × 75. (After Southwell.)

diameter of 300 μ and the posterior of from 180 to 200 μ. Accessory suckers are absent. Each bothridium bears anteriorly a pair of bifurcated hooks, the inner prong of which is longer than the outer and bears a rather large tubercle. Five hooks had the following measurements:—Total length, 140 to 170 μ; handle to bifurcation, 54 to 72 μ; inner prong, 90 to 105 μ; outer prong, 57 to 65 μ.

Neck. Shipley and Hornell state that the neck is 2 to 3 cm. in length, but in the specimens examined segments could be traced under a high magnification to a point 1·5 mm. behind the head.

Muscular System. Annular fibres appear to be absent, diagonal fibres are numerous. The longitudinal fibres are very strongly developed, and in cross-section consist of a single row of very large bundles running round the segment. The bundles on the dorsal and ventral surfaces are the largest,

and these have a length of about 130 μ and a breadth of 35 μ. The lateral bundles are smaller.

Excretory System. There are a pair of vessels running along each lateral margin; the dorsal one is smaller than the ventral, and the genital ducts run between them.

Nervous System. There is a single large nerve on each side lying external to the excretory vessels.

Testes. There are from about 15 to 20 testes on each side; when fully developed, each has a diameter of about 50 μ.

Vas deferens. The cirrus pouch lies postero-dorsally to the vagina and between the dorsal and ventral excretory vessels; in full development it measures about 170 by 70 μ. The terminal portion of the cirrus is dilated and thickly beset with small spines; the rest of the cirrus, and a portion of the vas deferens, lies coiled within the pouch. Outside the pouch the vas deferens is thrown into a large number of coils which

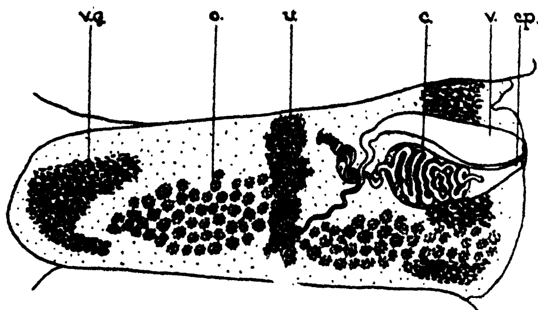


Fig. 135.—*Uncibilocularis trygonis.* Mature segment, × 75. (After Southwell.)

lie directly internal to the cirrus pouch; seminal vesicle apparently absent.

Ovary. The ovary does not appear until the testes are well developed. It is a bilobed organ situated posteriorly, the lobes at first being club-shaped. Eventually it becomes a massive organ composed of a number of large round acini, each of which has a diameter of about 50 μ.

Vagina. The vagina runs anteriorly and ventrally to the cirrus pouch and between the dorsal and ventral excretory vessels. At the median extremity of the latter organ it turns and runs in the middle line to the ovary. In front of the latter organ it is much coiled, and dilates into a rather inconspicuous receptaculum seminis.

Vitelline Glands. These are massive organs running the length of the segment and situated latero-externally to the excretory vessels.

Uterus. At first the uterus consists of a somewhat irregular mass running in the antero-posterior axis. A lumen soon appears and the walls become lobulated. In full development the uterus consists of a central portion from which there radiate laterally, anteriorly, and posteriorly a number of lobes which entirely fill the segment and present a rosette appearance. A minute uterine pore appears to open on the ventral surface.

Eggs. No fully ripe eggs were available; the ripest were either globular, having a diameter of 19 μ, or club-shaped, containing a segmenting ovum which measured 12 μ.

(2) **Uncibilocularis mandleyi** Southwell, 1927. (Figs. 136 & 137.)

From *Hemigaleus balfouri*, Pearl Banks, Ceylon. Pearson.

In all the specimens the neck is extremely delicate and elongated, and measures from 5 to 9 mm. in length and 60 μ in breadth. This is probably an artificial condition; normally



Fig. 136. *Uncibilocularis mandleyi.* A bothridium, × 75. (After Southwell.)

it probably measures only 1 or 2 mm. Excluding the neck, the worms measure from 1 to 1·5 cm., and the greatest breadth is about 180 μ; there are numerous segments, the last one measuring 240 μ in length and 160 μ in breadth.

All the specimens were immature.

Details of the nervous, muscular, and excretory systems are not known.

On account of certain peculiarities of the head the identification of this parasite is easy.

The head has a breadth (terminally) of about 1 mm.; posteriorly it is narrower. It bears four simple bothridia which are wider in front than behind; each bothridium measures about 850 μ in length and bears a very minute terminal loculus or sucker posteriorly, *i. e.*, at its free extremity. This peculiar organ is so small that it can only be seen when the bothridium is suitably mounted and examined with high-power magnifications. Anteriorly accessory suckers are entirely absent. Overhanging each bothridium is a pair of very characteristic bifurcated hooks, each having a long

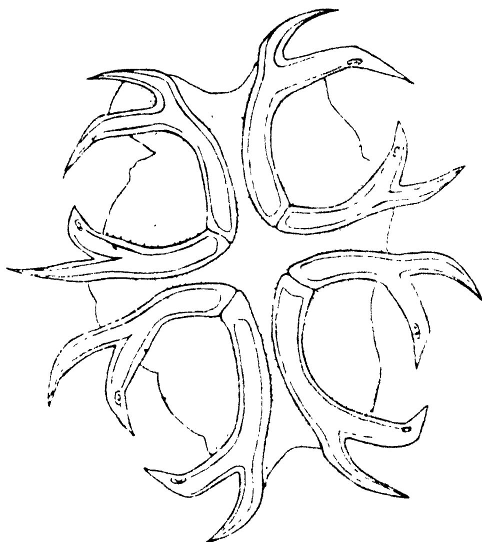


Fig. 137.—*Uncibilocularis mandleyi.* Head, viewed *en face*, × 75. (After Southwell.)

handle; the internal prong of each hook is longer than the external, and at a distance of about 100 μ from its extremity there is situated a peculiar vesicule in the body of this larger prong. In the largest head the hooks have the following measurements:—Total length of hook, 500 μ; handle to bifurcation, 340 μ; inner prong, 290 μ; outer prong, 180 μ.

Another peculiarity which the writer has not noted previously in any other species of cestode is the fact that not only did the heads vary in size within wide limits, but on the smaller heads the total length of the hooks was only 200 μ. Heads bearing hooks of a size intermediate between 200 and 500 μ have

been seen. It has not been usual, in the writer's experience, to find a growth series, with reference to hooks, in a collection of any species of cestode from any host.

The worm clearly belongs to the genus *Uncibilocularis*. It differs from *U. trygonis* Shipley & Hornell, 1906 (the only other species of this genus) in the size and shape of the hooks.

Genus V. PLATYBOTHRIUM Linton, 1890, emended.

Linton's original description of this genus, founded on one species, was :—" Body articulate, tæniæform, head decidedly flattened, squarish or trapezohedral. Bothria four, sub-triangular, sessile, arranged in marginal pairs, armed with compound hooks and each terminating posteriorly in a cup-like depression or loculus. A single indistinct circular depression (supplemental disc ?) on each bothrium in front of hooks. Genital apertures marginal."

Type-species :—*Platybothrium cervinum.*

The description by Linton of a second species necessitated the emendation of the characters of the genus as follows :—

Bothridia four, arranged in marginal pairs ; their surface is divided into three loculi by two septa ; each bothridium bears a pair of hooks, one of which is bifurcated and the other trifurcated.

Hornell (1923), apparently unaware that Linton had established the genus *Platybothrium* in 1890, erected another genus which he also named *Platybothrium*, with the following characters :—

" A tetraphyllid having four discoidal unilocular bothridia ; centrally situated between them is a stout, strongly muscular, prominent, anterior sessile sucker. The larvæ only are known."

Hornell also applied the name *Platybothrium sardinellæ* to a larva measuring about 1·5 mm. which occurs in the pyloric cæca of the Indian sardine (*Sardinella longiceps*). The larva apparently multiplies endogenously, for he states that the number of larvæ in each cyst varies greatly ; the smallest number was 2 and the greatest 183. The larva appears to be a specimen of *Scolex pleuronectis*. Only one species of this genus has been recorded from India.

(1) Platybothrium cervinum Linton, 1890. (Figs. 138, 139, & 140.)

Synonym :—*Platybothrium spinulifera* Southwell, 1912.

From *Galeocerdo arcticus*, Pearl Banks, Ceylon. Southwell.

The species was described from a single specimen which had the following dimensions :—Length, 6·7 cm. ; length of head, 520 μ ; greatest diameter of head, 540 μ ; length of

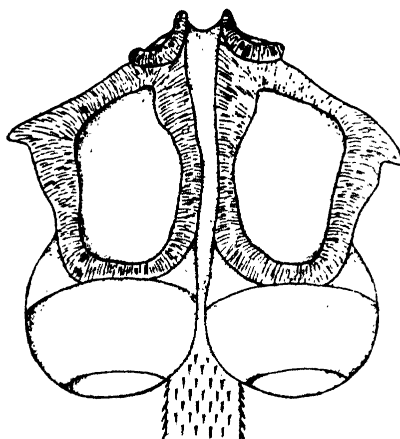
hooks, 160 μ; length of neck, 1·6 cm.; length of last segment, 1·4 mm.; breadth of last segment, 400 μ; length of cirrus pouch, 220 μ; breadth of cirrus pouch, 55 μ.

The worm is composed of a large number of segments; mature proglottides have not been seen. A full description of the genital organs has not been given, but Linton stated that (1) the ovary was bilobed; (2) the terminal part of the vagina was situated in front of the cirrus pouch; (3) the median

Fig. 138.



Fig. 139.



Platybothrium cervinum.

Fig. 138.—Hooks, × about 133. (After Linton.)
Fig. 139.—Head, × 160. (After Southwell.)

extremity of the vagina (near the ovary) was dilated; (4) the cirrus pouch was bent in the middle; and (5) the genital pores were marginal and near the middle (in his figure they are shown slightly anterior to middle).

Linton further states that "there appears to be a faint supplemental disc . . . although its identification in alcoholic specimens is not altogether satisfactory . . . with regard to the

occurrence of supplemental discs in this species, I am in some doubt. When the living worm was first examined . . . the anterior ends of the bothria were somewhat elongated and rounded, with a circular depression showing plainly in each. When I examined the specimen an hour or two later, in order to obtain measurements, the anterior ends of the bothria were abruptly truncated and there was no sign of circular depressions. . . . It would appear that the anterior ends of the bothria contract or fold inward, thus obscuring the faint depression, which is probably to be regarded as a supplemental disc."

He describes the posterior transverse costa of each bothridium as follows :—" In the sketches made of the living worm it appears to be a transverse costa which is convex towards the front, lying near the posterior end of the bothrium and

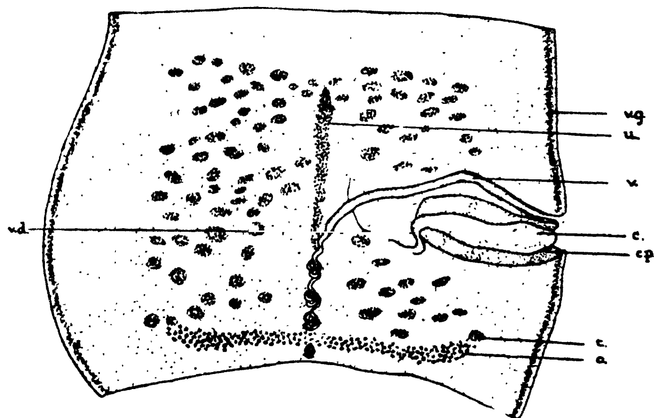


Fig. 140.—*Platybothrium cervinum.* Mature segment, × 160. (After Southwell.)

making a loculus in the face of the bothrium. In the alcoholic specimen, however, the appearance is somewhat different. Each bothrium appears to become somewhat tubular at its posterior extremity, and what, in the living specimen, appeared to be a posterior loculus now seems to be the thickened tubular end of the bothrium. The inner boundary of this tubular end extends farther back than the outer boundary, so that the appearance in a specimen which had been slightly compressed would, of course, be the same as if the bothrium were crossed by a transverse costa near the posterior end. The faces of the bothrium are but little hollowed out."

Minute spinules on the head, neck, and segments were first described in 1924. Discussing the systematic position of this form, Linton pointed out that the species is unique amongst armed Phyllacanthinæ in having a flattened head and marginal pairs of bothridia. At the same time he considered it allied to the genus *Prosthecobothrium*, from which he stated that it differed (1) in having accessory suckers, and (2) in the bothridia having a definite posterior loculus instead of a posterior sucker. Further, he concluded that the doubtful character of the accessory sucker, the shape of the hooks, and the fact that he was unable to decide definitely whether each bothridium was divided into two or three loculi, did not allow its inclusion in any of the three genera *Calliobothrium*, *Acanthobothrium*, and *Onchobothrium*. The flattened bothridia and their arrangement in marginal pairs were further considered by Linton to prevent its inclusion in the genera *Cylindrophorus* and *Phoreiobothrium*.

Platybothrium spinulifera Southwell, 1912.

The author in 1912 described under the above name a worm which was believed to differ from *P. cervinum* in being much smaller, bearing large numbers of minute spines on the head, neck, and parts of the strobila, in having hooks slightly different in shape from those of *P. cervinum*, and in the proglottides being broader than long, except the last three or four. The writer is now satisfied that *P. spinulifera* is identical with *P. cervinum* Linton.

The worm when alive measures 3·3 cm. in length and has a maximum breadth of about 600 μ, being composed of about 150 segments. The genital pores are irregularly alternate, situated either at the middle of the lateral margin or a little anteriorly or posteriorly to the centre. The largest posterior segment measures 530 μ in length and 270 μ in breadth. Except the last two or three proglottides, the entire worm is covered with spines.

Head. The head is almost square and measures about 350 μ. There are four bothridia: each bothridium measures about 270 μ in length and has a breadth of about 150 μ; its surface is split up into three loculi, but the posterior one is frequently very difficult to see. The anterior loculus occupies more than half the length of the bothridium and has strong muscular margins. The posterior one differs very markedly from the anterior in being a much more delicate structure and in the muscular margin either being absent or only slightly developed. Each bothridium bears a well-marked accessory sucker at its apex. The size and shape of the

hooks is not known. The entire head is densely covered with minute spines which measure about 13 to 18 μ.

Neck. The neck varies in length from 1·5 to 4 mm. and has a breadth of about 210 μ ; it is also densely covered with spines.

Muscular System. This is very feebly developed. The longitudinal musculature consists of a number of extremely minute bundles distributed throughout the cortical parenchyma. Circular fibres are practically absent ; a few discontinuous ones can occasionally be seen. The oblique muscles are more numerous.

Excretory System. There are two vessels running along the lateral margins, the dorsal one being much smaller than the ventral. The vagina and cirrus pouch run between them.

Nervous System. A very small nerve runs along each lateral margin externally to the water vessels.

Testes. The testes vary in number from about 42 to 90. On the pore side the number lying posteriorly to the cirrus is from 7 to 15, whilst anteriorly to that organ there are from 12 to 22. The remaining testes are situated aporally and anteriorly ; those in the anterior part of the segment are frequently smaller than the rest, and crowded together. The diameter of the largest mature testis is about 33 μ.

Vas deferens. The cirrus pouch in full development extends about one-third to one-fourth the distance across the segment ; it measures about 150 μ in length and 75 μ in breadth, and is situated posteriorly to the vagina ; it runs between the dorsal and ventral water vessels. The bend in the cirrus pouch described by Linton in *P. cervinum* was not seen in specimens of *P. spinulifera.* The unarmed cirrus is dilated and has glandular walls ; it occupies practically the whole of the pouch. The course of the vas deferens outside the pouch is short : immediately median to the latter it narrows to a very delicate coiled tube.

Ovary. This is situated posteriorly ; it is usually bilobed, but its appearance varies considerably according to the state of development and the contraction or elongation of the segment.

Vagina. From the ovary the vagina pursues a curved course to the pore, passing between the dorsal and ventral water vessels and opening anteriorly to the cirrus ; in contracted segments it is frequently thrown into small convolutions.

Shell Gland. This is a small round organ placed in the middle line behind the ovary.

Vitelline Glands. These are situated on each side immediately beneath the cuticle ; they extend the whole length of the segment except where interrupted by the cirrus pouch and vagina.

Uterus. Only the rudimentary organ has been described; it consists of a solid, densely granular mass extending in the median line from the ovary almost to the anterior extremity of the segment. Eggs unknown.

Genus VI. PEDIBOTHRIUM Linton, 1909, emended.

Synonym:—*Phyllobothroides* Southwell, 1911.

Linton defined this genus as follows:—"Body tenuiform, articulate, head separated from the body by a distinct neck, and provided with four distinct, cruciform armed bothria, without auxiliary suckers, costæ, or loculi. Each bothrium is strengthened by a strong muscular ring with a thin, more or less leaf-like border, and is armed at the anterior end with a pair of compound hooks. Each hook consists of two unequal prongs which rise from a flattened base. This basal part of the hook has a characteristic shape in each species. The neck is traversed by conspicuous bundles of longitudinal muscle fibres.

"This genus is separated from the genus *Acanthobothrium* by the absence of costæ, and from *Phoreiobothrium* by the character of the hooks, which have two instead of three prongs, and further by the absence of loculi on the bothria. . . ."

Type-species:—*Pedibothrium globicephalum* Linton, 1909, from *Ginglymostomum cirratum*.

In order to accommodate a species of the genus *Pedibothrium* which possesses rose-thorn-shaped hooks it is necessary to emend the characters of the genus as follows:—

Head consists of four simple, undivided, leaf-like bothridia armed with simple or compound hooks.

Key to Species.

1. Hooks rose-thorn-shaped	*P. hutsoni*, p. 282.
Hooks bifurcated, not rose-thorn-shaped .	2.
2. Total length of hook 35 μ	*P. globicephalum*, p. 276.
Total length of hook 150 to 212 μ; small worms with only 10 to 30 segments . .	*P. longispine*, p. 279.

(1) **Pedibothrium globicephalum** Linton, 1909. (Figs. 141, 142, 143, & 144.)

From *Pristis cuspidatus*, Pearl Banks, Ceylon. Pearson.

Linton describes this species as follows:—"Head, especially in preserved specimens, globular. Bothria ovate, projecting in front of hooks, and supplied with prominent marginal border; each armed with a pair of small two-pronged hooks. The prongs are only moderately curved and are of unequal size, the inner one being the shorter. The common base is somewhat

elongated. . . . Genital cloaca on lateral margin, a little behind the middle; vagina in front of the cirrus, at first at right angles to the axis of the segment, then parallel with it to the paired ovaries near the posterior end of the segment.

Fig. 141.

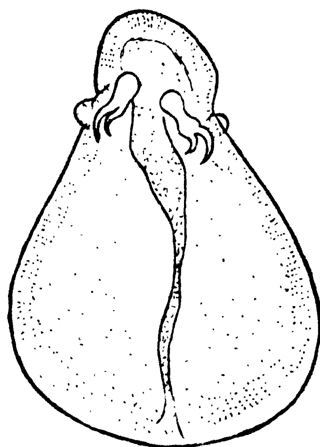


Fig. 142.



Pedibothrium globicephalum.

Fig. 141. - A bothridium, × 72. (After Linton.)
Fig. 142. - A hook, × 250. (After Southwell.)

"The vitelline glands form a marginal border throughout, except at the extremities. As a rule they extend but a short way back beyond the ovaries. . . . The uterus is spacious and lies between the ovary and the angle of the vagina. The ova are

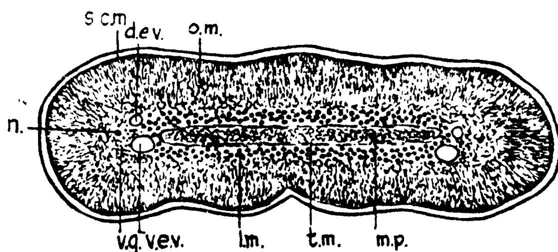


Fig. 143. - *Pedibothrium globicephalum.* Transverse section of immature segment, showing musculature, × 160. (After Southwell.)

amber colour, thin shelled, mostly collapsed, and consequently difficult to measure. The cirrus is long, slender, enlarged at the base, with exceedingly minute spines, if any. Testes numerous, occupying the middle space in front of the vagina.

Cirrus pouch behind vagina and in its angle, but most of the coils of the vas deferens are in front of the vagina. Length in life as much as 60 mm.

"Dimensions of a mounted specimen in millimetres: Length, 30; head (compressed), length, 0·96; bothrium, length 0·80; breadth, 0·40; breadth of neck, 0·56; distance to first segment about 1·6; free segments with ripe ova, length 1·8, breadth 0·6; length of hooks, 0·035; ova about 0·025 and

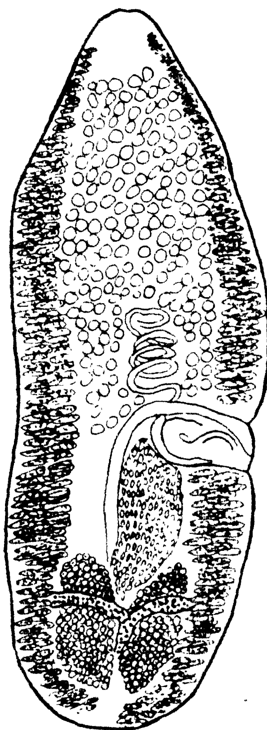


Fig. 144.—*Pedibothrium globicephalum*. Mature segment, × 50. (After Linton.)

0·018 in the two principal diameters. This species was found on three occasions in the spiral valve of the nurse-shark. . ."

The following additional details were obtained from the examination of two immature specimens from Ceylon.

Head. The hooks have the following dimensions:—Large prong, including base, 144 μ, excluding base, 65 to 70 μ; small prong, including base, 126 μ, excluding base, 36 to 40 μ. In other respects the head agrees with Linton's description;

the genital pore lies slightly behind the centre of the lateral margin of the segment.

Muscular System. The cuticle has a thickness of about 4 μ, and immediately beneath it there is a prominent layer of subcuticular fibres. Dorso-ventral ones are also prominent and numerous. The circular muscles are feebly developed and can only be seen with difficulty. The longitudinal musculature consists of a single layer comprising a large number of small bundles, each having a diameter of about 10 μ, distributed irregularly.

Excretory System. There are two vessels on each side, one being directly ventral to the other; the ventral vessel is much larger than the dorsal.

Nervous System. There is a single small nerve lying laterally to the excretory vessels on each side.

Testes. There are a large number of testes; on the pore side of the middle line, none occur posteriorly to the cirrus pouch. Only the rudiments of the latter organ and the vas deferens are known, the former extending to the middle of the segment.

Ovary. This lies posteriorly, the rudiments observed presenting a bilobed appearance; the vagina was not developed, but the rudiment of the uterus was seen extending anteriorly from the ovary, in the middle line.

(2) **Pedibothrium longispine** Linton, 1909. (Figs. 145 & 146.)

Synonym.—*Phyllobothroides kerkhami* Southwell, 1911.

From *Chiloscyllium indicum*, *Galeocerdo arcticus*, and *Rhina ancylostoma*, Pearl Banks, Ceylon. Southwell.

The following is an abstract of Linton's description of this species:—" Bothria in life elongate, with crenulate borders in fresh specimens, flexible, often reflected. . . . Hooks relatively long, in some cases equal to half the length of a bothrium. The two hooks on each bothrium have their bases apposed and projecting forward to the anterior end of the bothrium. The two prongs on each hook are long as compared with the oblong base, and are strongly recurved; the outer prong is about the size of the inner, and both are curved in the same manner, so that the two would lie in the same curved surface and be nearly parallel. . . . The neck exhibits various contraction stages in life, but at rest appears to be slightly larger than the succeeding part of the strobile. In the mounted specimens it was seen to be minutely spinose and distinct from the body, with strong longitudinal muscle bundles of relatively course strands. Strobila, so far as certainly seen, filiform. . . . Details of the anatomy were not certainly made out for ripe segments, but are probably much like those

of *P. brevispine*. The two species may be distinguished from each other by means of the hooks, which present quite marked differences besides that of size. From the nurse-shark (*Ginglimostoma cirratum*). . . . All small, with no mature segments.

"Dimensions of living specimens in millimetres: Head, length 0·35; breadth 0·35; bothria, length 0·35, breadth 0·21; length of hooks, base not included, larger 0·06, smaller 0·03; diameter of neck 0·09: distance to first distinct segment 0·42: number of segments 9; last segment, length 0·63, breadth 0·06. In two mounted specimens the length of the

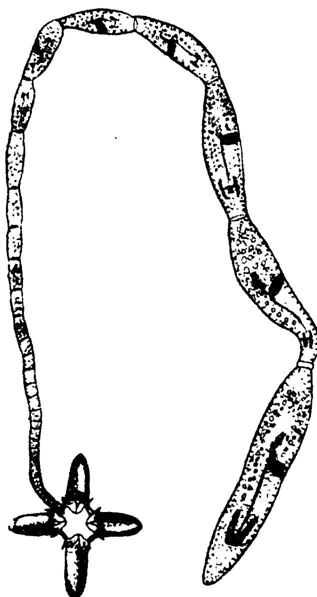


Fig. 145.—*Pedibothrium longispine*. Entire worm, × 18. (After Southwell.)

bothrium in each was 0·35, and the hooks, including the base, 0·15."

The author in 1911 described this species under the name *Phyllobothroides kerkhami*; the worm measures 1·5 cm. in length and contains about 28 segments; the head bears 16 hooks in pairs. The last segment is very variable in size, the largest (detached) measuring 4 mm. in length and 540 μ in breadth. The genital pores are irregularly alternate, and are situated near the middle of the lateral margin of the proglottid.

Head. The head is about 400 μ in length and 340 μ in breadth. The bothridia are very variable in length, as would

be expected from their great mobility in life. In preserved specimens the largest measured about 750 μ in length and 150 μ in breadth. Near the anterior margin of each bothridium there is a pair of bifid hooks (fig. 146) having the following dimensions :—Total length, 184 to 212 μ ; handle to point of bifurcation, 72 to 82 μ ; outer prong, 112 to 140 μ ; inner prong, 83 to 98 μ.

Neck. This measures from about 230 to 300μ in length. Details of the muscular, excretory, and nervous systems were not investigated ; a number of broad muscular bands were noted running to the bothridia.

Testes. These number about 70, and each testis has a diameter of about 32 μ. They lie practically in two single rows, one along each lateral margin, the aporal reaching posteriorly to the ovarian lobe and the poral not extending backwards to the genital pore. In front of the latter there are a few testes scattered irregularly between the two rows.

***Vas** deferens.* The cirrus pouch lies behind the vagina and has a length of about 72 μ and a breadth of 32 μ.

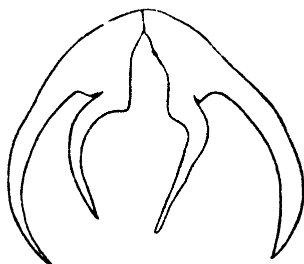


Fig. 146. —*Pedibothrium longispine.* A pair of hooks, × 160. (After Southwell.)

The cirrus is not spiny ; when protruded it measures 530 μ in length and 75 μ in breadth ; it has a bulbous base lying outside the pouch. The vas deferens is a conspicuous coiled tube which, from the median extremity of the cirrus pouch, runs forwards in the axis for a distance of about 160 μ. No seminal vesicle was observed.

Ovary. This lies posteriorly and consists of two lobes, united by a narrow isthmus of ovarian tissue. Each lobe is very long (300 μ) antero-posteriorly, and also very narrow (30 to 35 μ).

The vitelline and shell glands, the uterus and vagina, resemble those described in *P. hutsoni*, and call for no comment. No gravid segments were seen ; the last proglottid in every worm contained ripe male and female genitalia only. From observations made on living material the author is of opinion

that the mature proglottides are detached and become gravid in the lumen of the intestine. An enormous number of detached segments of very large size, and showing great movement, were frequently seen in the intestine of fish, but it was almost impossible to identify the parasite.

In 1911 the author, unaware of Linton's paper, created the genus *Phyllobothroides* with the following characters:—"Head with four simple undivided bothridia, which are slightly concave. Overhanging the proximal part of each bothridium is a pair of simple or bifurcated hooks. Neck fairly long. Proglottides not salient. Cuticle ringed throughout." He also described two species, viz., *Phyllobothroides kerkhami* and *Phyllobothroides hutsoni*, but is now satisfied that the genus *Phyllobothroides* is identical with Linton's genus *Pedibothrium*, and it therefore becomes a synonym of the latter genus; also, as noted above, the species *kerkhami* is synonymous with *longispine*. *Phyllobothroides hutsoni* Southwell, 1911, differs however, from other species within the genus in possessing rose-thorn-shaped hooks.

(3) **Pedibothrium hutsoni** (Southwell, 1911) Southwell, 1924. (Figs. 147 & 148.)

Synonym:—*Phyllobothroides hutsoni* Southwell, 1911

From *Ginglymostoma concolor*, *Galeocerdo articus*, and *Rhina ancylostoma*, Pearl Banks, Ceylon. Pearson; Southwell.

The largest worm measured 6·7 cm. in length and the greatest breadth was 650 μ: the last segment, which was ripe (but not gravid) was 1·4 mm. in length and 750 μ in breadth. The lateral margins of the parasite are perfectly

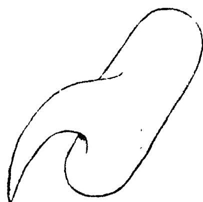


Fig. 147.—*Pedibothrium hutsoni*. Hook. × 250. (After Southwell.)

straight, the junction of the segments not being marked by any irregularity. The genital pores are irregularly alternate, being situated very slightly in front of the middle of the lateral margin. The total number of proglottides present in the largest mature (but not gravid) worm is over 100.

Head. The greatest breadth is about 800 μ; it is a little difficult to say precisely what the length is, owing to the fact that it merges almost imperceptibly into the neck. In one or two cases where an approximate measurement was possible it was about 760 μ. The four bothridia each measure about 680 μ in length and about 300 to 350 μ in breadth. Their anterior rims are very muscular, and in contracted preserved specimens resemble slightly the suckers of a typical *Tænia*, having the posterior borders incomplete.

Within the anterior margin of the acetabulum-like thickening there are two rose-thorn-shaped hooks in each both-

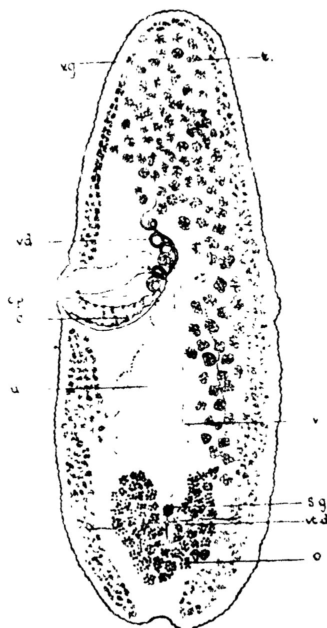


Fig. 148.—*Pedibothrium hutsoni*. Partly gravid segment, × 160. (After Southwell.)

ridium. Each one consists of a basal portion measuring 70 to 90 μ in length and 30 μ in breadth. From this, and a little nearer one extremity than the other, a curved tapering hook arises, terminating in a fine point. It measures 45 to 60 μ in length. The total length of the base and of the hook is about 110 μ.

Neck. This varies in length, but usually measures about 7 mm.

Muscular System. The muscular system is strongly developed. In the neck region the longitudinal bundles are disposed in

two irregular layers; between them the dorso-ventral fibres are well developed. More posteriorly, however, when the testes appear, only a single layer of large bundles can be seen. Circular muscles are scanty, but oblique ones are everywhere prominent.

Excretory System. There are two vessels running along each lateral margin, the dorsal being smaller than the ventral.

Nervous System. There is a single nerve along each lateral margin, situated externally to the excretory vessels.

Testes. These vary in number from about 80 to 130, and each testis has a diameter, when fully mature, of about 54 μ. The largest number is situated in front of the pore; on the aporal side they extend posteriorly to about two-thirds the length of the segment. There are no testes on the pore side behind the cirrus pouch.

Vas deferens. The cirrus pouch measures about 130 μ in length and 30 μ in breadth. It extends in a direct line towards the middle of the segment, and its walls are thick and densely studded with nuclei. The cirrus is dilated and armed with innumerable fine hooks. The vas deferens lying outside the pouch is a long convoluted tube, which forms a number of coils immediately median and anteriorly to the internal extremity of the pouch. Its walls are also densely studded with nuclei, and, like the cirrus, it is covered with fine spines throughout most of its length. No external seminal vesicle was observed.

Ovary. This is a bilobed organ situated quite posteriorly, the two lobes being connected by a long narrow bridge of ovarian tissue. Each half, when fully mature, measures about 130 μ in the antero-posterior direction and 80 μ transversely. The connecting isthmus measures about 70 μ and has a thickness of about 16 μ.

Vagina. From the pore the vagina always passes in front of the cirrus pouch; rounding the median extremity of which it curves sharply and then runs directly backwards, passing between the lobes of the ovary. Here it dilates into a small receptaculum seminis; slightly behind this organ the uterus arises. The vagina then bends sharply through 180° and becomes confluent with the oviduct; the latter runs forward and opens to the uterus about the level of the pore.

Shell Gland. This lies posteriorly between the two wings of the ovary; it is a rounded organ having a very granular appearance.

Vitelline Glands. These extend the whole length of the lateral margin of the segment except where interrupted by the cirrus pouch and vagina. The acini are rather small (about 20 μ) and lie laterally, five or six deep, on each side. Two ducts occur posteriorly, one from each side, and these, uniting in the middle line, open to the fertilisation canal.

Uterus. At first the uterus is a simple tube arising between the two wings of the ovary and running forwards in the middle line. Later on a number of lateral pouches arise from this central stem, and these also enlarge until the uterus fills the entire segment. Ripe eggs have not been observed.

Table showing the Principal Characters of the three Indian Species of Pedibothrium.

	Pedibothrium globicephalum.	*Pedibothrium longispine,* after Linton.	*Pedibothrium longispine,* after Southwell.	*Pedibothrium hutsoni.*
Length of worm.	1·6 to 6 cm.	Small.	1·5 cm.	7 cm.
Breadth of worm.	600 μ	60 μ	540 μ	650 μ
Length of neck.	1·6 mm.	Spinose, 420 μ.	300 μ	8 mm.
Number of segments.	Numerous ?	9	About 28.	Over 100.
Length of hooks.	144 μ	150 μ	184 to 212 μ	45 to 60 μ. Base 70 to 90 μ by 30 μ.
Inner prong	36 to 40 μ	30 μ	83 to 98 μ	—
Outer prong	65 to 70 μ	60 μ	112 to 140 μ	—
Remarks	Head globular, bothridia with prominent margins.	No mature segments seen.	With mature segments.	Rose-thorn-shaped hooks.

Genus VII. **YORKERIA** Southwell, 1927.

The characters of this genus are here emended as follows :—Head with four armed bothridia, in pairs ; each bothridium oval or circular and divided into two loculi, one of which is very large and the other very small. Each bothridium bears a pair of U-shaped hooks, unequal in size, one being situated near each lateral extremity of the septum The genital pores are irregularly alternate and situated near the middle of the lateral margin of the segment.

Type-species :—*Yorkeria parva* Southwell, 1927.

Yorkeria parva Southwell, 1927. (Figs. 149 & 150.)

From *Chiloscyllium indicum,* Pearl Banks, Ceylon. Pearson.

This species was originally described from three heads and one immature specimen. Since the account was written, a

number of fully mature specimens have been obtained from the same host and locality.

The worm measures up to 1·2 cm. in length and is frequently twisted upon itself. It attains a breadth of about 230 μ and is composed of at least 70 segments. The genital pores are irregularly alternate and situated near the middle of the lateral margin, but in mature segments in the anterior third.

Head. There are four bothridia, in pairs, each pair borne on a rather long stout pedicel, the two pedicels uniting into a common trunk, the whole frequently resembling the letter Y

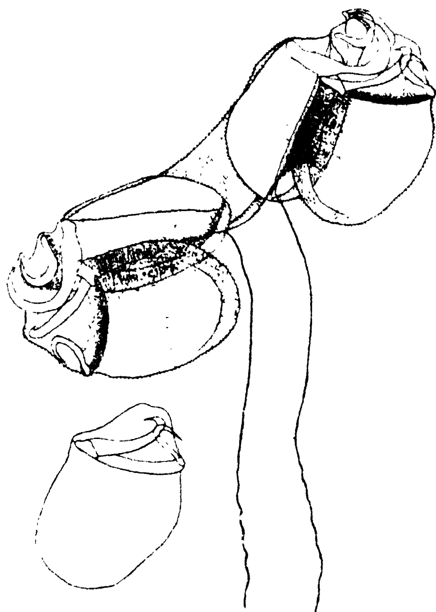


Fig. 149.—*Yorkeria parva.* Head and a bothridium × 60. (Original.)

or T in shape. In the original specimens the bothridia appear undivided, a circumstance which has since been found to be due to the fact that they are somewhat folded upon themselves. In the new material each bothridium is quite definitely divided by a single septum into two unequal loculi, the distal one being much the smaller. The bothridia may be circular or oval, and are thickened at the point of attachment to the pedicel. The entire surface of the head is covered with innumerable minute spines which have a length of about 10 μ. Each bothridium is armed with a pair of U-shaped hooks, these being very unequal in size and situated one near the

lateral extremity of the septum. The hooks have the following dimensions :—

Large Hook.

Length of long limb................	200 to 260 μ
Length of short limb	about 110 μ
Distance between the two limbs............	150 μ
Breadth of root............................	50 μ

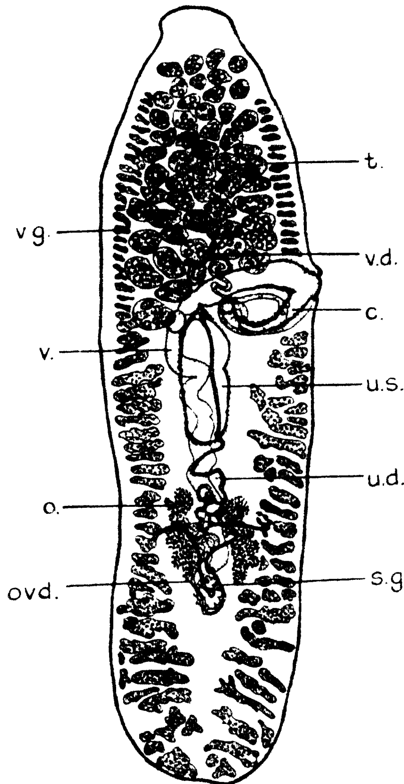


Fig. 150.—*Yorkeria parva.* Segment, × 48. (Original.)

Small Hook.

Length of long limb................	105 to 116 μ
Length of short limb...............	75 to 80 μ
Distance between the two limbs.....	80 to 90 μ
Breadth of root	about 25 μ

There are about 50 testes, each having a diameter of from 45 to 90 μ ; they occupy the entire segment anterior to the

cirrus pouch, but do not extend posteriorly to it on either side. The latter organ is conspicuous and runs almost to the middle of the segment; it contains a few coils of the vas deferens. Outside the pouch the vas is rather convoluted and runs in the anterior direction. The cirrus is armed with minute spines. The cirrus pouch and vagina open into a well-defined genital atrium.

The position of the ovary varies according to the degree of maturity. At first it lies posteriorly, but in fully mature segments it is near the junction of the middle and posterior thirds of the proglottid. It consists of four elongated lobes, two on each side of the median longitudinal axis: in each pair one lobe lies immediately dorsal to the other. The vagina is a very wide duct throughout its entire length. From the pore it extends anterior to the cirrus pouch to the middle of the segment. It then swings backwards and becomes slightly sinuous. The oviduct runs posteriorly as a long, curved, narrow duct, turning forwards again and running through the shell gland, which latter organ is situated behind the ovary. Anterior to the shell gland it continues as the vagina, giving off proximally a minute tube, the uterine duct, which latter dilates near the cirrus pouch into a well-defined, cylindrical, thick-walled bag—the uterine sac. The vitelline glands consist of groups of large acini extending along the whole length of the lateral margins of the segment. In the vicinity of the ovary a vitelline duct from each side runs in the median direction; they unite into a common vessel which posteriorly opens to the oviduct at the shell gland.

Genus VIII. **THYSANOCEPHALUM** Linton, 1889.

Synonym:—*Myzocephalus* Shipley & Hornell, 1906

Linton's definition of the genus is as follows:—"Body articulate, tæniæform. Head separated from body by neck, very small, quadrangular, with four sessile bothria, each armed with two simple hooks and provided with a single loculus in front of the hooks. Neck at first slender, then expanding into a voluminous mass of lobed and crisped folds. Genital apertures marginal."

Type-species:—*Thysanocephalum crispum* (Linton, 1889).

The characters of the genus are emended as follows:—

Head small consisting of four sessile bothridia each divided into two loculi and armed with two simple hooks. A pseudoscolex is present.

As Linton's species *T. ridiculum* does not possess a pseudoscolex it is placed in the genus *Ceratobothrium*.

Thysanocephalum crispum (Linton, 1889). (Figs. 151, 152, 153, & 154.)

Synonyms:—*Phyllobothrium thysanocephalum* Linton, 1889 (renamed *T. crispum*).
Thysanocephalum thysanocephalum (Linton, 1889) Braun, 1900.
Myzocephalus narinari Shipley & Hornell, 1906.

From *Stoasodon narinari*, Pearl Banks, Ceylon. Hornell; Southwell.

Linton first described the worm under the name *Phyllobothrium thysanocephalum*, but a little later made it the type of a new genus (*Thysanocephalum*). In 1892 he gave a very full account of the anatomy.

The worm measures up to 1 m. in length, and has a maximum breadth of about 7 mm. The genital pores are irregularly

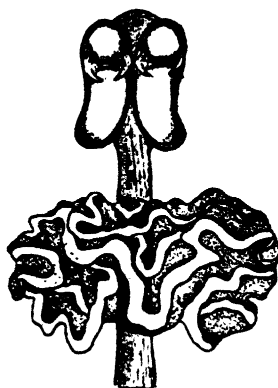


Fig. 151.—*Thysanocephalum crispum*. Head and pseudoscolex, × 46. (After Southwell.)

alternating, and are situated a little behind the centre of the lateral margin. The last segment often measures 8 mm. in length and 4·5 mm. in breadth.

Head. The head is very small, being only about 350 to 380 μ in length and 350 to 400 μ in breadth. It consists of four small sessile bothridia, each measuring about 220 μ in length and 160 μ in breadth, and divided into two loculi. The margins of the bothridia are thickened and muscular, being marked with transverse striations. Each anterior loculus is small and has muscular rims also with transverse striæ; the posterior edge on each side is produced into a solid, pointed, chitinous spine. These spines (of which there are two to each bothridium) measure about

72 μ in length, and they all point towards the longitudinal axis of the bothridium.

Neck. The head is succeeded by the first portion of the neck. This measures about 200 to 250 μ in length, and it has a breadth of about 90 μ. It is terminated posteriorly by a large pseudoscolex which ranges from 700 μ to 1·2 mm. in length and from 1·2 to 1·5 mm. in breadth. It consists of a massive fleshy "collar," ruffled and frilled, resembling somewhat closely the heads of *Phyllobothrium lactuca* and *P. foliatum.* This pseudoscolex is followed posteriorly by the second part of the neck. Linton states that in one specimen this portion of the worm measured 480 mm. Its length, however, varies within very wide limits, and depends on the size of the worm. The surface of the second part of the neck appears scaly under low-power magnifications.

Muscular System. This is well developed. The longitudinal musculature is seen in transverse sections to consist of a very

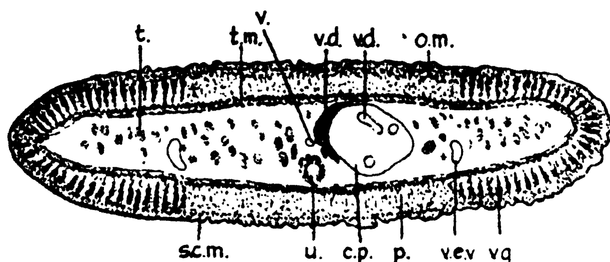


Fig. 152.—*Thysanocephalum crispum.* Transverse section of mature segment, × 28. (After Southwell.)

large number of small bundles densely and irregularly crowded together into a single layer. Median to the longitudinal muscles is a layer of circular fibres having a thickness of about 20 μ. Externally to the longitudinal muscles the cortical parenchyma is well developed, and traversed by numerous strands of oblique fibres. A layer of well-defined cuticular muscles is situated immediately beneath the cuticle.

Excretory System. There are two lateral vessels on each side, the dorsal one being much smaller than the ventral and situated directly laterally to it, In the posterior segments the cirrus pouch and vagina run dorsally to the ventral excretory vessel, but all traces of the dorsal excretory vessel have disappeared.

Nervous System. There is a single nerve running along each lateral margin externally to the two water vessels.

Testes. In a mature proglottid over 900 testes can be counted, and each has a diameter of about 72 μ.

Vas deferens. The cirrus pouch is very large, and is situated behind the vagina. The cirrus is long, dilated, and has thickened walls thrown into transverse rugosities; its terminal part is cup-shaped and armed with a few spines. The vas deferens is narrower than the cirrus, and a number of coils lie within the cirrus pouch. Outside the pouch the vas deferens forms a very large number of coils in the median line between the internal extremity of the cirrus pouch and the anterior prolongation of the vagina. There is no seminal vesicle, and the coils of the vas deferens undoubtedly act as a reservoir.

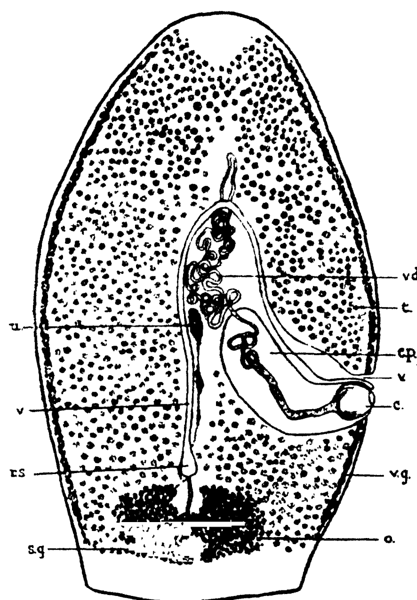


Fig. 153.—*Thysanocephalum crispum.* Mature segment, × 18. (After Southwell.)

Ovary. The ovary is a large, prominent, bilobed organ situated posteriorly, composed of rounded and club-shaped acini.

Vagina. The vagina lies in front of the cirrus pouch; its terminal portion is dilated, and its walls are thrown into numerous transverse rugosities. From the pore it runs inwards to the median line. It then bends suddenly and runs backwards in the antero-posterior axis; at the anterior extremity of the ovary it narrows considerably, and at this point the uterus arises and runs forwards. The narrowed

portion, which is the fertilization canal, is continuous with the common oviduct, and it receives the ducts of the vitelline and shell glands. No special receptaculum seminis is present, but the vagina gradually dilates as it approaches the ovary, and the dilated portion may be regarded as a receptaculum.

Vitelline Glands. These lie along the lateral margins, extending the whole length of the segment except where interrupted by the cirrus pouch and vagina; even in ripe proglottides they are not prominent. They consist of isolated oval follicles measuring about 44 by 22 μ. The vitelline ducts arise posteriorly and, converging in the middle line, unite and open into the fertilization canal.

Shell Gland. This is a globular organ situated quite posteriorly between the two wings of the ovary. It measures about 160 μ in diameter and consists of a number of club-shaped acini radiating from a central portion. Its duct opens into the fertilization canal.

Uterus. Gravid segments have not been described. The uterus arises immediately behind the receptaculum seminis and runs forward as a tube which presents a beaded appearance. Linton states that as the uterus ripens the ventral wall of the segment becomes thin, and eventually dehiscence takes place. Eggs are unknown.

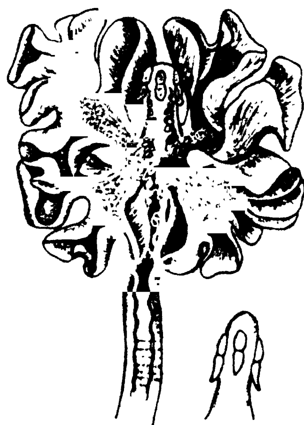


Fig. 154.—*Thysanocephalum crispum.* Head, × about 27. (After Shipley and Hornell.)

Myzocephalus narinari Shipley & Hornell, **1906.**

Shipley and Hornell erected the genus *Myzocephalus* with the following characters :—" 'Head' with four slipper-shaped bothridia, each divided by a horizontal partition into two areolæ. 'Head' surrounded and smothered in four most

voluminous and crumpled folds like the bothridia of *Anthobothrium*. Proglottides barrel-shaped. Reproductive organs irregularly alternate. Cuticle finely ringed." This genus is obviously identical with Linton's *Thysanocephalum*. Shipley and Hornell described one species only, viz., *M. narinari* (probably a young form). Their account and figures leave no room for doubt that *M. narinari* is the same worm as *Thysanocephalum crispum* Linton.

Fig. 155.

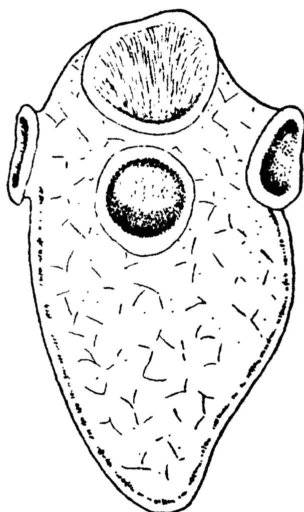


Fig. 156.



Scolex pleuronectis. (After Southwell.)

Fig. 155, × 20.
Fig. 156, × 18.

Scolex pleuronectis Müller, 1788. (Figs. 155 & 156.)

Synonym :—*Scolex polymorphus* Rud., 1819.

From *Sardinella longiceps*, Indian ocean and tidal rivers of India. Southwell.

Specimens in all stages of development have been found, the largest measuring 1 mm. in length and having a maximum

breadth of 400 μ. The larvæ often have the form of an isosceles triangle, the broad end being anterior. There are four suckers arranged round the anterior extremity, and a very prominent terminal sucker which is larger than the other four suckers. The body is finely pigmented and calcareous corpuscles are present. In a few specimens the head was invaginated, as in Cysticercus cellulosæ, but in the great majority it was evaginated.

Superfamily IV. LECANICEPHALOIDEA, nov.

Linton in 1890 suggested that the three genera *Discocephalum* Linton, 1890, *Lecanicephalum* Linton, 1890, and *Tylocephalum* Linton, 1890, should be referred to a new family, for which he proposed the name Gamobothriidæ, but whose characters he did not define. As there is no genus *Gamobothrium*, Linton's name cannot stand.

Braun (1900) divided the order Tetraphyllidea into four families, viz., Onchobothriidæ, Phyllobothriidæ, Ichthyotæniidæ, and Lecanicephalidæ (= Gamobothriidæ Linton), the latter containing the three genera noted above. In the first two families, the head in each species bears four bothridia, but in the latter two bothridia are absent, and the head bears four suckers. For this reason the writer, in 1925, transferred the families Ichthyotæniidæ (=Proteocephalidæ La Rue, 1911) and Lecanicephalidæ to the order Cyclophyllidea Braun, 1900, emended. This latter order he split into two suborders, viz., Univitellata and Multivitellata; in the latter he placed the families Proteocephalidæ La Rue, 1911, and Lecanicephalidæ Braun, 1900.

Poche (1926) adopts Braun's family Lecanicephalidæ.

Woodland (1927) discussed the family Lecanicephalidæ Braun, and concluded, from the disposition of the muscular system and from the fact that the vitelline glands are lateral, that a number of genera now placed in that family belong to the Phyllobothriidæ, and he proposed, subject to certain species he named being ultimately proved to be phyllobothrids, that the genera *Lecanicephalum*, *Cephalobothrium*, *Balanobothrium*, *Polypocephalus*, and *Calycobothrium* be included in the Phyllobothriidæ. Of the two remaining genera of the family Lecanicephalidæ, *Adelobothrium* and some species of the genus *Tylocephalum* are referred by him to the Tetrarhynchidæ, whilst other species of the genus *Tylocephalum* are not relegated to any family, and he proposes awaiting the results of further investigation before attempting their classification.

Pintner (1928) splits up the family Lecanicephalidæ into four families, namely, Discocephalidæ, Tetragonocephalidæ, Cephalobothriidæ, and Balanobothriidæ.

The characters of the superfamily are the following:—Scolex armed or unarmed, bearing four suckers as in the superfamily Tænioidea. Genital organs arranged as in the superfamilies Phyllobothrioidea and Tetrarhynchoidea, *i. e.*, the acini of the vitelline glands are scattered and not condensed into a single gland, except in one species.

Family LECANICEPHALIDÆ Braun, 1900.

Synonyms:—Gamobothriidæ Linton, 1889.
Polypocephalidæ Meggitt, 1924.
Nec Lecanocephalidæ Diesing, 1861.

Braun defined the characters of the family as follows:—"The bothridia are fused into a globe-shaped plate; accessory suckers may be present or absent; neck long, short or absent; genital pores marginal; found in elasmobranch fishes." As this definition appeared inadequate in the absence of any evidence that the bothridia were ever separate, and as a number of other genera closely related to *Tylocephalum* have been described since 1900, the characters were emended by the writer in 1925 as follows:—

Head with four suckers and composed of two portions; the anterior part may be either globular, flattened antero-posteriorly and retractile or not, or split into tentacular processes; when retractile it functions as a terminal sucker sunk deep in the head; it may bear either suckers or hooks, or both, or these structures may be absent. The posterior part may be either subglobular, collar-like, or split up into tentacular processes, and it may bear suckers or hooks, or both, or these structures may be absent. Genitalia as in Phyllobothrioidea except, so far as is known, in one species in which the vitelline gland is single and posterior; genital pores ventral or lateral; uterine pores present or absent.

Type-genus:—*Lecanicephalum* Linton, 1890.

In the various genera included in this family the head presents a most interesting and important series of modifications which we will now consider. In the genus *Cephalobothrium* it is subglobular and bears four suckers; its anterior extremity is occupied by another sucker which is enormous and cup-shaped. This sucker can be—but rarely is—evaginated; but, when protruded, the head is exactly similar to that of a species of *Tylocephalum*. The real difference between the heads in the two genera is that in *Cephalobothrium* the myzorhynchus is normally invaginated and functions as a deep sucker, whilst in *Tylocephalum* it is normally evaginated. In *Tylocephalum* both the myzorhynchus and the head proper are almost always subglobular, whilst

in *Lecanicephalum* they are flattened antero-posteriorly, so that the head consists of two disciform plates, the anterior one having ruffled margins and the posterior part bearing four suckers. In the genus *Discocephalum* the head is very similar to that in *Lecanicephalum*, but it differs in suckers being absent. The worm is further peculiar in that the vitelline gland is single and situated behind the ovary. In *Adelobothrium* the posterior part of the head is membranous and collar-like, and the anterior part (myzorhynchus) is either cylindrical or conical, with a rounded truncated extremity. In *Balanobothrium*, also, the posterior part of the head is membranous and almost cup-shaped, the myzorhynchus being large and subglobular. A further important difference in this genus is that the suckers are not borne on the posterior part of the head as in all other genera except *Calycobothrium*, but on the anterior part (myzorhynchus). Close to each sucker is a pair of minute compound hooks.

In the genera *Calycobothrium* and *Polypocephalus* tentacles are present. In the latter genus the tentacles may be considered as the myzorhynchus which has become split up, whilst in the former genus the myzorhynchus is intact and bears suckers (as in *Balanobothrium*) and the tentacles probably represent subdivisions of the posterior part of the head.

Genitalia. The only points of outstanding importance in the arrangement of the genitalia have reference to the position of the genital pore and the vitelline glands. In all species within the family the genital pores are marginal, except in *Tylocephalum uarnak* Shipley & Hornell, 1906, and the vitelline glands are either bilateral or extend across the entire dorsal and ventral surfaces except in the latter worm, where the gland is single.

Key to Genera.

1. Head armed with four pairs of minute bifid hooks	BALANOBOTHRIUM, p. 335.
Head not armed with hooks	2.
2. Head with tentacles	3.
Head without tentacles	4.
3. Tentacles arise behind the head	CALYCOBOTHRIUM, p. 348.
Tentacles arise from a deep fossa in the anterior face of the head	POLYPOCEPHALUS, p. 342.
4. Myzorhynchus present	5.
Myzorhynchus absent	6.
5. Anterior and posterior parts of head more or less subglobular	TYLOCEPHALUM, p. 306.
Anterior and posterior parts of head flattened antero-posteriorly (plate-like)	LECANICEPHALUM, p. 297.
Anterior part of head cylindrical or conical: posterior part membranous and collar-like	ADELOBOTHRIUM, p. 330.
6. Head with a terminal sucker	CEPHALOBOTHRIUM, p. 299.
Head without terminal sucker	STAUROBOTHRIUM, p. 350.

Each of the genera *Calycobothrium*, *Lecanicephalum*, and *Adelobothrium* contains one species only.

The descriptions of *Tylocephalum ludificans* Jameson, 1912, and *T. ætobatidis* Shipley & Hornell, 1906, are so inadequate that these species cannot be identified. *T. minus* Jameson, 1912, was described from an encysted larva, and the adult is not known.

Genus I. LECANICEPHALUM Linton, 1890
(*nec* LECANOCEPHALUS Diesing, 1839 (=GOEZIA Zeder, 1800)).

Linton's definition of this genus was as follows :—" Body tæniæform, articulate, head transversely flattened, circular or subquadrangular, and consisting of two disciform plates. Posterior plate with four supplementary disks (auxiliary suckers). Neck short or none. Genital apertures marginal."

Type and only species :—*Lecanicephalum peltatum* Linton, 1890.

Linton pointed out that his genus was closely related to, if not identical with, *Discobothrium* van Ben., 1870. He provisionally placed the genera *Lecanicephalum* and *Tylocephalum* in the Tetrabothriidæ, but stated that it might be necessary subsequently to refer them in a distinct group, for which he proposed the name Gamobothriidæ.

Lecanicephalum peltatum Linton, 1890. (Fig. 157.)

From *Pristis cuspidatus*, *Dasybatus kuhli*, and *Pteroplatea micrura*, Pearl Banks, Ceylon. Southwell.

The worms, which are not fully mature, measure about 1·7 cm. in length, and the greatest breadth varies from 200 to 400 μ. The head has a breadth of about 900 μ and a length of from 200 to 300 μ. Other measurements correspond with those given by Linton for his specimens.

The neck measures from 1 to 2 mm. in length ; the first segments are practically linear, and they increase in length slowly. The last one measures about 550 μ in length and 170 μ in breadth. There are about 150 proglottides, in addition to a number immediately behind the neck which cannot be counted. The genital pores are somewhat irregularly alternate, and situated in the anterior half of the segment in immature ones and in the anterior third in those nearing maturity.

Muscular System. The longitudinal fibres are arranged in stout bundles which in cross-section radiate outwards, decreasing in size towards the periphery. Oblique or circular muscles have not been described.

Excretory System. In whole mounts a small vessel can be seen on each side running a little lateral to the mid-line.

Posteriorly, owing to the development of the genitalia, they cannot be seen. In cross-section these vessels lie in the mid-transverse line, and, in addition, two other much smaller ones occur frequently, but not invariably.

Testes. There are sixteen or seventeen testes, and they occupy the whole of the middle field in whole mounts. At first they are cylindrical, with somewhat pointed extremities, lying with their long axes parallel to the transverse diameter of the segment. When fully mature they are globular, and each has a diameter of about 45 μ.

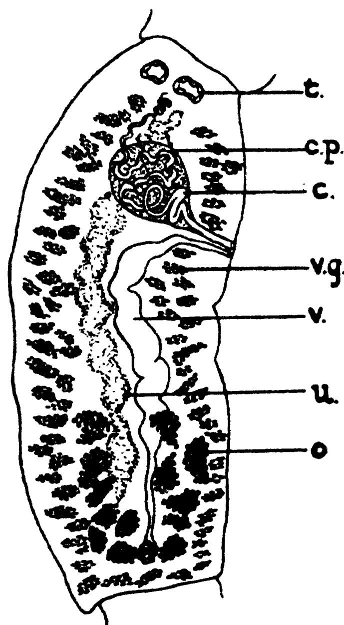


Fig. 157.—*Lecanicephalum peltatum.* Mature segment, × 112. (After Southwell.)

Vas deferens. The cirrus pouch is a large structure in the anterior half of the segment, measuring about 450 μ in diameter and 380 μ in length. It extends halfway across the segment, and is at a little distance from the lateral margin, communicating with the pore by a narrow duct. The cirrus lies in several loose coils inside the pouch, and no armature was seen. The vas deferens is extremely short, and a seminal vesicle is absent.

Ovary. The ovary is situated along the posterior margin of the segment; the vagina is figured above.

Vitelline Glands. These consist of from twelve to fourteen acini along each lateral margin. Each acinus measures only about 18 μ in diameter.

Uterus. The uterus is immature, and consists of a tube with slightly lobulated walls running along the antero-posterior axis. No eggs have been seen.

Genus II. **CEPHALOBOTHRIUM** Shipley & Hornell, 1906.

The characters of this genus are as follows :—"A large median circular sucker takes up most of the head ; it is controlled by longitudinal muscles. Four small spherical suckers are placed equidistant from each other in the rim of the circular sucker. The proglottides are wider than broad, with the exception of the last six or seven. The reproductive pores are lateral and very irregularly alternate." (*Shipley & Hornell.*)

Type-species :—*Cephalobothrium ætobatidis* Shipley & Hornell, 1906.

In 1912 the author described two other species, *C. variabile* and *C. abruptum.* Whilst the centre of the head is almost always occupied by a large circular sucker having various shapes, the sucker is capable of being protruded and, when extended, the head resembles that of a species like *Tylocephalum pingue* or *T. dierama.* Several preserved heads have been seen with the sucker fully protruded, and thus transformed into a myzorhynchus. In view of this fact, it seems probable that the two genera, *Tylocephalum* and *Cephalobothrium*, are closely related, the principal difference between them being that in most species of the genus *Tylocephalum* the myzorhynchus is permanently protruded, whereas in the three species referred to the genus *Cephalobothrium* the myzorhynchus is usually withdrawn and disappears, being transformed into a deep cup-like circular sucker.

Key to Species.

1. Small forms about 10 mm. in length	*C. ætobatidis*, p. 299.
Large forms up to 12 cm. in length	2.
2. Over 60 testes ; ovary dumbbell-shaped	*C. abruptum*, p. 300.
Less than 30 testes ; ovary of radiating club-shaped acini	*C. variabile*, p. 304.

(1) **Cephalobothrium ætobatidis** Shipley & Hornell, 1906. (Fig. 158.)

From *Stoasodon narinari*, *Pteroplatea micrura*, and *Dasybatus kuhlii*, Pearl Banks, Ceylon. Hornell ; Southwell.

Shipley and Hornell described the worm as follows :—'This curious cestode was drawn from life by Mr. Hornell,

in Ceylon; the enormous terminal sucker being, in that state, much more conspicuous than in the preserved material. This sucker is round with thickened edges, and from its underside run longitudinal bands of muscles which apparently control it. The whole head is rounded, shaped like a turban, and bears four minute spherical suckers on the edge of the great median terminal sucker. There is no neck. The proglottides begin immediately after the sucker.

"The whole length of the single worm we had at our disposal was 10 mm., but the posterior proglottides seemed ripe; the breadth of the head and of the posterior proglottides is 0·5 mm., the rest of the body is very fine and slender. The proglottides remain broader than they are long until within the last six;

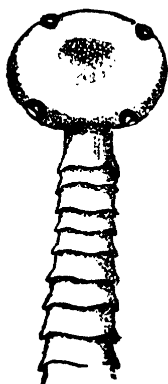


Fig. 158.—*Cephalobothrium ætobatidis*. Head, × about 40. (After Shipley and Hornell.)

here they become square, and the last of all is almost twice as long as broad. The posterior angles of each proglottis overlap the anterior rim of the succeeding one, but not to a pronounced degree. The reproductive openings are very irregularly alternate and lateral."

(2) **Cephalobothrium abruptum** Southwell, 1911. (Figs. 159, 160, 161, & 162.)

From *Pteroplatea micrura* and *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

The worms, which are composed of numerous segments, measure about 12 cm. in length, and they have a maximum breadth of about 1·5 mm. The last ones measure 1·2 mm. in length and about 700 μ in breadth. Genital pores irregularly alternate and situated laterally in the anterior third of the segment; worm oval in cross-section.

Head. The head resembles that of *C. ætobatidis*; it is egg-shaped, and measures 1·3 mm. in length and about 1·2 mm. in breadth. It is really made up of two parts; the anterior extremity is occupied by a large protrusible sucker which is succeeded by a basal part shaped like a truncated cone. having the broad base forward; this bears four minute suckers with swollen lips, slightly raised above the surface, situated two on each side and each has a diameter of about 230 μ. The appearance of the head varies considerably, according to the extent to which the terminal sucker is protruded. It will be obvious that if the terminal sucker is fully extended. as it sometimes is, it becomes a rostellum or myzorhynchus. The head is then similar to that of *Tylocephalum pingue*.

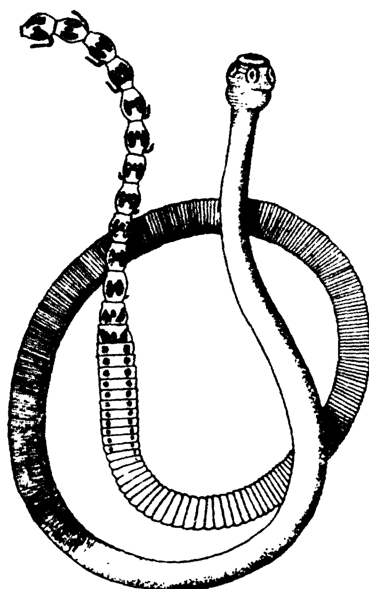


Fig. 159.—*Cephalobothrium abruptum.* Entire worm, × 4. (After Southwell.)

Neck. It is impossible to say whether a neck is present or not; the wrinkling of the cuticle behind the head appears to pass by imperceptible gradations into the short anterior segments.

Muscular System. This is strongly developed. A series of broad muscle bands passes to the head. In the anterior part of the worm the longitudinal muscles consist of a large number of single bundles, radiating to the exterior. When the genitalia, and especially the uterus, are developed, these bundles become short and disposed in two rows, the internal one

being much more strongly developed than the external, which latter is somewhat irregular. Oblique fibres are fairly numerous, but circular ones are scanty.

Excretory System. This consists of two very small vessels on each side—a dorsal and a ventral. They are only evident in the anterior portion of the strobila; in ripe segments they cannot be seen.

Nervous System. There is a single nerve on each side running lateral to the water vessels.

Testes. The number of testes varies considerably; usually there are about forty-five situated aporally, and from twenty-two to twenty-eight on the pore side; there are no testes in

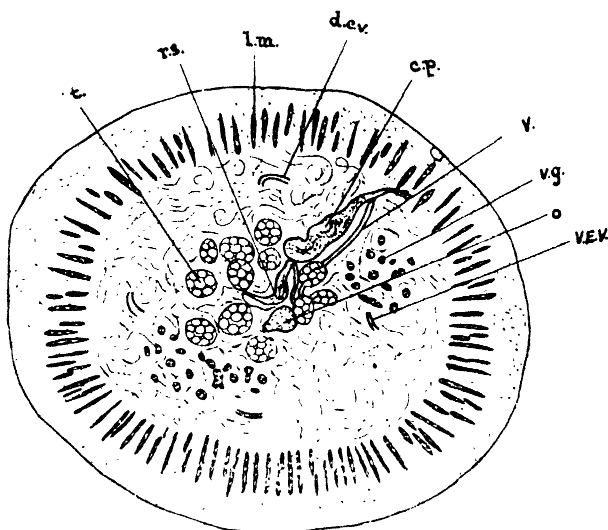


Fig. 160.—*Cephalobothrium abruptum.* Transverse section of nearly mature segment, × 74. (After Southwell.)

front of the cirrus pouch; each testis when fully developed has a diameter of about 50 μ.

Vas deferens. The cirrus pouch measures about 180 μ in length and about 120 μ in breadth; its internal margin reaches to the middle of the segment. The cirrus is unarmed; the vas deferens is very long and lies in several large coils within the pouch; outside the latter it runs anteriorly and is coiled; no seminal vesicle was seen.

Ovary. The ovary differs from that of *C. variabile* in being dumbbell-shaped, much more massive, and in not being composed of radiating columns. It measures about 400 μ across.

Vagina. This is a very wide muscular tube at least 300 μ in length and 70 μ in breadth when fully developed. Its walls are characterized by peculiar markings which at first give the impression of a number of very fine spines arranged in a series of closely set spirals, but no spines are present; the appearance

Fig. 161.

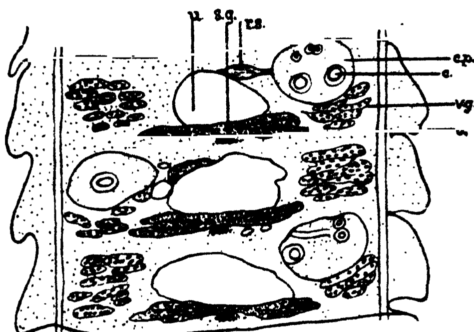
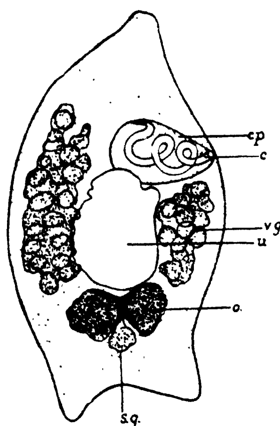


Fig. 162.



Cephalobothrium abruptum.

Fig. 161.—Horizontal section of mature segment. × 74. (After Southwell.)
Fig. 162.—Nearly gravid segment, × 74. (After Southwell.)

is due entirely to circular muscle fibres. From the pore it runs behind the cirrus pouch, then, rounding the internal extremity of the latter organ, it proceeds (in a sinuous course in young segments) directly to the centre of the ovarian isthmus, where it dilates into a small receptaculum seminis.

Vitelline Glands. These are similar to those described for *C. variabile*, but are more massive and do not consist of cylindrical, but of globular acini.

Uterus. This arises like that of *C. variabile*, and has the same form.

Eggs unknown.

(3) **Cephalobothrium variabile** Southwell, 1911. (Figs. 163 & 164.)

From *Pristis cuspidatus* and *Dasybatus kuhli*, Pearl Banks, Ceylon. Southwell.

The worm measures up to 13 cm. in length and about 600 μ in breadth; it is made up of over four hundred segments.

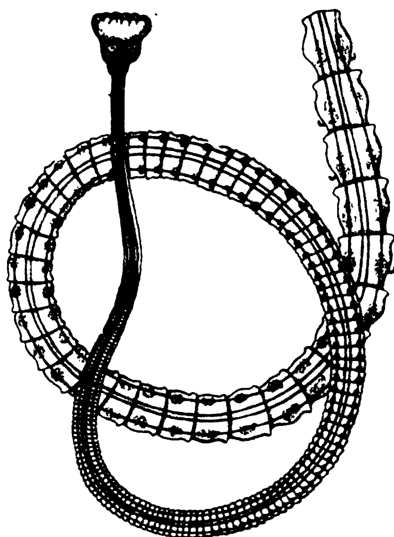


Fig. 163.—*Cephalobothrium variabile.* Entire worm, × 8. (After Sonthwell.)

The genital pores are irregularly alternate and are situated in the anterior third of the lateral margin of the segment.

Head. This resembles the head of *C. abruptum* Southwell, 1911, and measures about 750 μ in length and 1 mm. in breadth. Anteriorly the head terminates in a deep, wide sucker occupying almost the whole of the anterior surface, and extending posteriorly about one-third to one-half the length of the head. The margin of this terminal sucker is somewhat thickened, and bears four (not two, as originally stated) small subsidiary suckers. Occasionally the sucker is protruded, and the head then resembles that of *Tylocephalum pingue.*

Neck. This varies in length, being usually about 1 mm.

Muscular System. As in *C. abruptum.*

Excretory System. Two vessels of equal size run along each lateral margin ; they are close together, one being immediately dorsal to the other.

Nervous System. As in *C. abruptum.*

Testes. These vary in number from about fourteen to eighteen, and occupy the whole of the central dorsal field. Most frequently they are cylindrical, with somewhat pointed ends, lying with their long axes at right angles to the length of the worm ; each measures about 60 by 20 μ. Occasionally, when very mature, they are globular, each having a diameter of about 75 μ. They persist until the uterus develops.

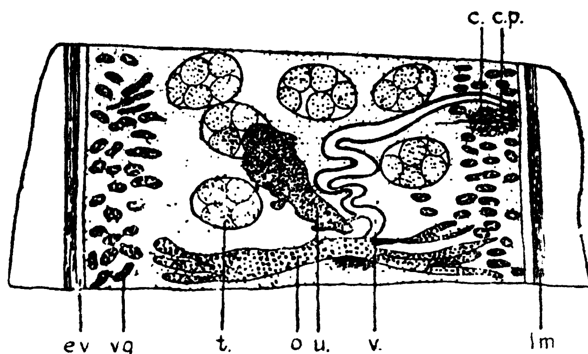


Fig. 164.—*Cephalobothrium variabile.* Horizontal section of mature segment, × 160. (After Southwell.)

Vas deferens. The cirrus pouch is almost globular, and lies for the most part internal to the water vessel, the communication to the exterior being by a narrow duct. The vas deferens is a short wide tube following a zig-zag course.

Ovary. This is situated posteriorly and consists of from about four to six cylindrical lobes on each side, lying at right angles to the long axis of the worm. Each one in full development measures about 120 μ in length and 40 μ in breadth. The lateral edges of the ovary appear embedded in the vitelline glands. The lobes on each side are connected by a very long and slender bridge of ovarian tissue.

Vagina. From the pore the vagina runs in front of the cirrus pouch and pursues a curved and somewhat irregular course backwards to near the centre of the ovarian isthmus, where it dilates into a small seminal vesicle. It is very muscular, the circular fibres giving to it characteristic herring-bone markings.

Vitelline Glands. These consist of a number of very large acini, each one being about 75 μ in length and 40 μ in breadth, situated laterally and lying also at right angles to the long

axis of the worm. They only reach their maximum size when the uterus is well developed. Their ducts unite in the median line and open into the fertilization canal.

Uterus. This commences as a narrow tube with thick walls, arising posteriorly, and extends in a sinuous course anteriorly to near the middle line. In ripe segments it occupies the entire central portion of the proglottid, being bounded laterally by the large vitelline gland. It is evident that at this stage of their development the segments are shed, and become gravid in the lumen of the intestine.

Eggs unknown.

Genus III. TYLOCEPHALUM Linton, 1890.

Synonyms:—*Tetragonocephalum* Shipley & Hornell, 1905.
Kystocephalus Shipley & Hornell, 1906.
Aphanobothrium Seurat, 1906.

Linton defined the genus as follows:—" Body articulate; head globose; bothria united into a globular disk and bearing four supplemental disks which are arranged in lateral pairs; myzorhynchus also globose, as large as remainder of head. Neck, *i. e.*, unjointed anterior part of body, moderately long."

The characters of the genus have been emended as follows:— Body articulate; head composed of a large globular or subglobular myzorhynchus, which is unarmed, and a posterior globular or subglobular part, the head proper, which bears four suckers. Genital pores marginal except so far as is known in one species.

Type-species:—*Tylocephalum trygonis* Shipley & Hornell, 1906.

Key to Species.

1. Myzorhynchus very much smaller than posterior part of head	*T. translucens*, p. 320.
Myzorhynchus about same size as posterior part of head	2.
2. Vitelline glands bilateral	3.
Vitelline gland single and posterior to ovary	*T. uarnak*, p. 321.
3. Genital pore small, uterus not dumbbell-shaped	4.
Genital pore very large, uterus dumbbell-shaped	5.
4. Worms 8 cm. in length, oval in cross-section; each segment with about 30 testes	*T. yorkei*, p. 325.
Worms 3·5 cm. in length, flat, each segment with about 50 testes	*T. dierama*, p. 311.
5. Genital pore ventral in anterior segments; with 38 to 63 testes; axis of cirrus pouch antero-posterior	*T. minutum*, p. 325.
Genital pore always lateral; testes 7 to 12; axis of cirrus pouch not antero-posterior.	*T. trygonis*, p. 307.

(1) **Tylocephalum trygonis** (Shipley & Hornell, 1905) Shipley & Hornell, 1906. (Figs. 165, 166, 167, & 168.)

Synonym:—*Tetragonocephalum trygonis* Shipley & Hornell, 1905.

From (1) *Dasybatus walga*, Pearl Banks, Ceylon. Hornell. (2) *Dasybatus* sp. (? *kuhli*), Chilka Lake, Orissa, India. Southwell.

According to these authors the worm is fragile. The head forms a distinct knob, borne on a slender neck; its diameter

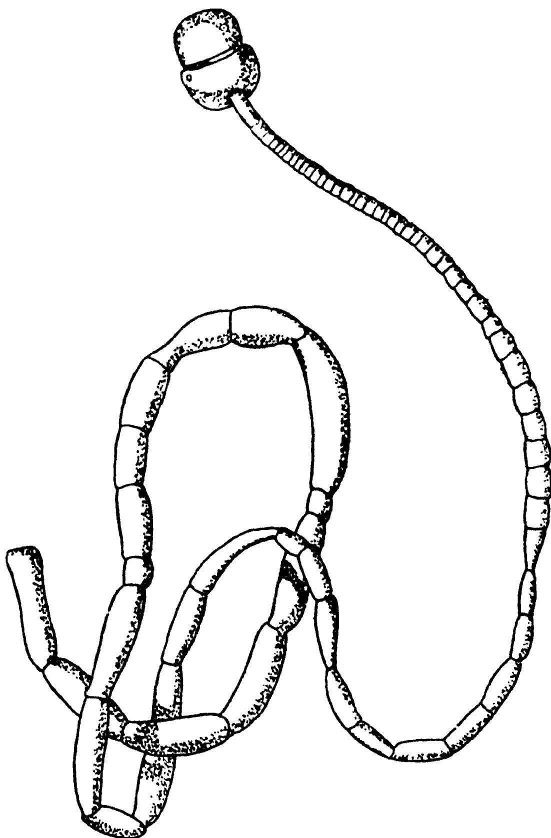


Fig. 165.—*Tylocephalum trygonis*. Entire worm, × 24. (After Shipley and Hornell.)

is 300 μ and its antero-posterior axis is slightly less, but may be greater than the transverse diameter. It consists of two parts, viz., an anterior unarmed circular and rounded knob, resting on a square cushion which carries a sucker at each of its corners. From these suckers small papillæ protrude,

passing through the orifice. There is a short neck; the last segments are much longer than broad. The genital pores are lateral and the penis lies concealed in a spacious recess. The pores are irregularly alternate. At its first appearance the uterus seems double, but the two parts are in communication by a narrow channel. The whole uterus is dumbbell-shaped and the eggs are slightly oval. The specimens examined by the writer measure about 2·7 cm. in length and the greatest breadth is about 800 μ. They consist of from fifty to seventy segments, counted under a microscope; of these about twenty are situated immediately behind the head, and are invisible to the naked eye. The last ones measure up to about 3 mm.

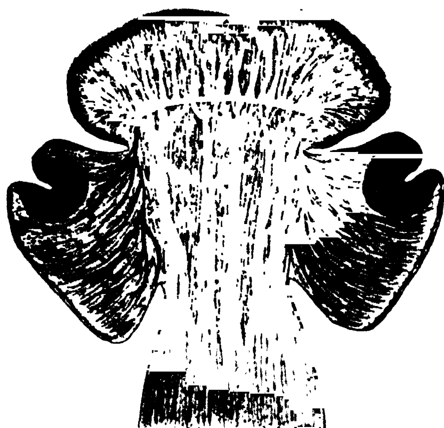


Fig. 166.—*Tylocephalum trygonis.* Horizontal section of head, showing spinules and musculature, × 160. (After Southwell.)

in length and have a breadth of about 270 μ. The genital pores are of enormous size, being surrounded by a large scalloped frill. They are irregularly alternate, and are situated behind the middle of the lateral margin. The posterior and lateral edges of the segments are straight, not salient. There is no neck, segmentation beginning immediately behind the head.

Head. This varies in size considerably; in one specimen it measured 260 μ in length and 330 μ in breadth. It consists of two parts, viz., an anterior myzorhynchus, shaped like a half-sphere and armed with innumerable minute spines 10 μ in length, and a posterior rounded portion, the head proper, which bears four suckers, but is devoid of spines. The papillæ mentioned by Shipley and Hornell have not been observed since. The head resembles closely that of *Tylocephalum pingue* Linton, which occurs in American waters.

Strong muscles run to the head and spread out fanwise in the myzorhynchus, and laterally a well-defined layer of subcuticular fibres is very prominent. Nothing is known regarding the excretory and nervous systems. The rudiments of the genital cloaca, running transversely, are visible immediately behind the head in the tenth or eleventh segment; in the fourteenth and fifteenth segments there is a particularly well-defined receptaculum seminis. The cirrus pouch and genital sucker develop very late.

Testes. These vary in number from about seven to twelve, and are situated anteriorly; frequently they are distributed in the form of the letter U inverted. They are only to be found in about segments 26 to 32; at this stage the

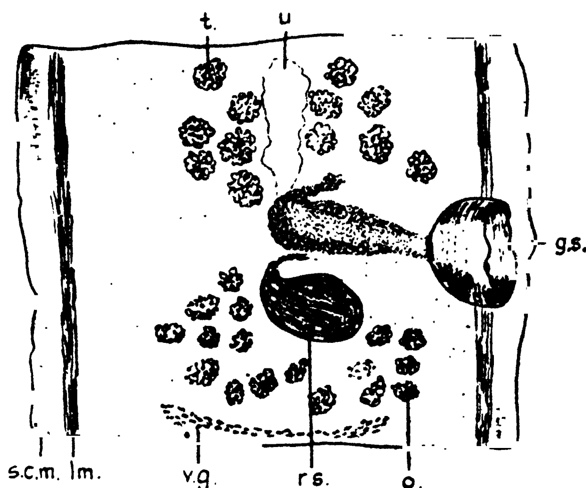


Fig. 167.—*Tylocephalum trygonis.* Mature segment. × 250. (After Southwell.)

genital cloaca and the duct connecting the latter with the cirrus pouch are but ill-defined, and are represented by a dense granular mass. The cirrus pouch is first seen as a hollow vesicle lying almost in the median line of the segment, and quite independent of the large genital cloaca. It enlarges very slowly, and is not fully developed until the uterus contains eggs. It then measures about 165 μ in length and 100 μ in breadth; it lies well within the segment, occupying the middle half or two-thirds, and communicates with the very large genital atrium, noted before, by a rather long and dilated duct. The pore itself is enormous, and is surrounded by a sucker with a collar-like frill having scalloped margins which can be seen with the naked eye; it is situated in the posterior half

of the lateral margin. The cirrus is coiled and long, and is apparently not covered with spines. A few coils of the vas deferens can be seen lying within the fully-developed cirrus pouch, but outside this organ it dilates into a very muscular seminal vesicle which usually lies parallel and directly anterior to the pouch.

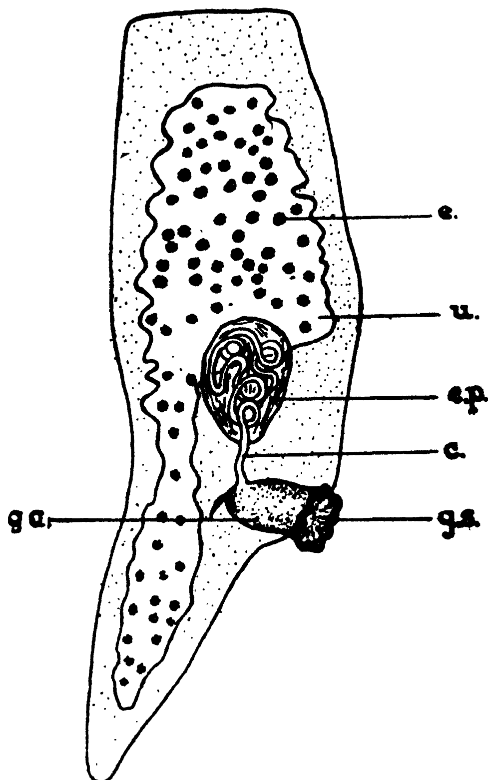


Fig. 168.—*Tylocephalum trygonis*. Gravid segment, × 112. (After Southwell.)

Ovary. This is a massive organ situated quite posteriorly, and is usually only found in about six or seven segments, viz., those which contain the testes.

Vagina. Owing to the large size of the cirrus pouch and seminal vesicle, it is not known with certainty whether the vagina passes anteriorly or posteriorly to the pouch; it appears to open at the base of the genital cloaca. It runs

posteriorly in the median line to the front of the ovary, where it dilates into the very large receptaculum seminis, which, as noted above, appears in about segment 12. It disintegrates with the ovary.

Shell Gland. This is a small globular organ lying between the receptaculum and the ovary.

Vitelline Gland. This species is strikingly peculiar in that the vitelline gland begins to develop behind the ovary. It is a very small, bilobed organ, each half being club-shaped; later it extends forwards along the lateral margins.

Uterus. The uterus appears early, and can be clearly seen in segments which contain the testes as a tube with irregular walls running between the testes and situated anteriorly. It develops suddenly and contains eggs in the first segment in which the ovary has atrophied. In full development it is a simple sac occupying the whole of the segment and consisting of two parts, viz., a portion behind, and a larger portion in front of, the cirrus pouch. The two are connected together by a very narrow tubular part which runs on the aporal side of the cirrus pouch.

Eggs. These are large, somewhat scanty, and occur in quite a number of posterior segments. The largest immature eggs are globular and measure 50 μ.

As the anatomy of *T. pingue* Linton has not been described, it is impossible to identify Linton's worm, and it therefore cannot be compared with any of those described below; it may, or may not, be identical with any of them. *T. trygonis* Shipley & Hornell, 1905, was the next species to be described, and it therefore becomes the type-species of the genus.

(2) **Tylocephalum dierama** Shipley & Hornell, 1906. (Figs. 169, 170, 171, 172, & 173.)

Synonyms:—*Tetrarhynchus unionifactor* Shipley & Hornell, 1904, *pro parte*.
Tylocephalum kuhli Shipley & Hornell, 1906.
Tylocephalum ludificans Jameson, 1912.
Tænia acanthobothria MacCallum, 1921.

From (1) *Ætomylæus maculatus*, *Dasybatus kuhli*, and *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Hornell; Southwell. (2) *Stoasodon narinari*; larvæ from the pearl oyster (*Margaritifera vulgaris*), Pearl Banks, Ceylon. Jameson; Herdman and Hornell; Willey.

The original description of this species was as follows:—

"Along with *Rhoptrobothrium myliobatidis*, a specimen or two of what we take to belong to Linton's genus *Tylocephalum* were found. The worms measured between 20 mm. and 35 mm. They were very slender anteriorly, but the posterior proglottides attain a width of 0·5 mm., and the head is about

0·5 mm. in breadth, and is rather longer than broad. The head consists of an anterior cushion, called a myzorhynchus by Linton ; it is obviously to some extent retractile, and in one of our specimens was slightly 'pulled in' in the middle, so that the whole head resembled a cottage loaf. This myzorhynchus is separated from the second part of the head or 'bothrial disc,' as Linton has it, not only by a constriction, but by a narrow band. The 'bothrial disc' is spherical and bears four equidistant simple suckers. There is a short neck. The proglottides are, at the posterior end, not more than twice as long as they are broad. They are flattened. Anteriorly they have salient posterior borders, and these, as they approach the hinder end, become much more conspicuous, and overhang an eighth or a sixth of the length of the succeeding proglottis. These funnel-like extensions are very characteristic of this species; they are much less marked in Linton's species,

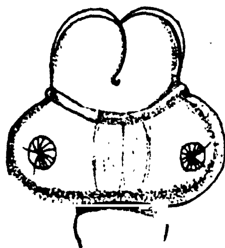


Fig. 169.—*Tylocephalum dierama*. Head, magnification unknown. (After Shipley and Hornell.)

T. pingue. The last proglottides were equally rounded and contained a uterus full of ova." (*Shipley & Hornell.*)

The largest worms measure 2·5 cm. in length and the greatest breadth is 560 μ. There is a very short neck varying from 500 μ to 1·2 mm.

The anterior proglottides are so shallow that it is impossible to determine where they commence. The worm is composed of over four hundred segments, counted under a high-power magnification. A large number of the anterior ones are very short; in those containing testes the lateral margins overlap about half of the succeeding segment, but, as they elongate, the lateral imbrication becomes correspondingly less conspicuous. The last two or three segments in each worm are barrel-shaped. The measurements of the terminal proglottid in six different worms vary from 600 to 825 μ in length and from 320 to 610 μ in breadth. The genital pores are irregularly alternate and are situated very slightly behind the middle of the lateral margin except in the last two or

three segments, where, owing to the elongation of the posterior portion of the proglottid, they lie in the anterior half.

Head. The head varies in shape considerably. Similar variations are encountered in other species of this genus; it consists of a large subglobular anterior myzorhynchus which does not bear either spines or hairs, and a posterior cushion-like portion which carries four suckers. It varies in length from 124 to 250 μ and in breadth from 160 to 230 μ. The

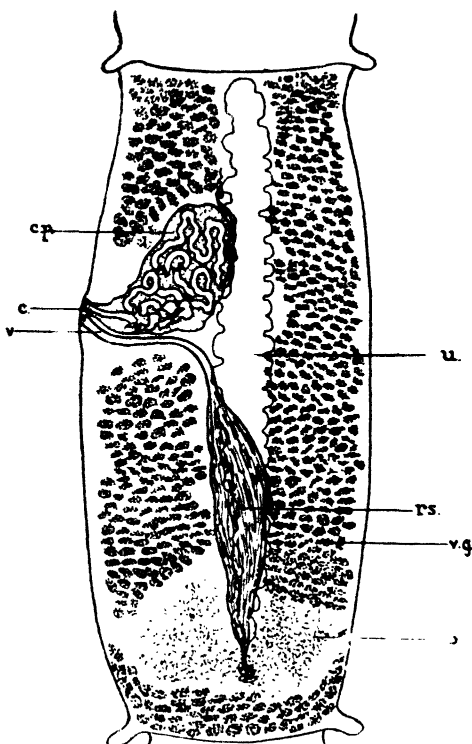


Fig. 170.—*Tylocephalum dierama.* Mature segment, × 75. (After Southwell.)

myzorhynchus is from 25 to 80 μ in length and in breadth from 90 to 145 μ. Each sucker has a diameter of about 55 μ.

The muscular, excretory, and nervous systems have not been described. The genital organs first appear about 250 segments (700 to 800 μ) behind the head.

Testes. There are about fifty testes; when fully developed they appear to occupy the entire segment in whole mounts. Each one has a diameter of about 55 μ.

Vas deferens. The cirrus pouch is not conspicuous; it is situated anteriorly to the vagina; in full development it measures about 120 by 90 μ. The cirrus is short and apparently unarmed; a few coils of the vas deferens lie within the pouch; seminal vesicle absent (?).

Ovary. The ovary is situated quite posteriorly, and is a bilobed organ composed of very small, elongated, club-shaped acini radiating fanwise on each side. Later on it enlarges considerably, and the acini frequently become indistinct.

Vagina. The vagina opens posteriorly to the cirrus pouch; in a mature segment it is a very short tube dilating close to the median extremity of the cirrus pouch into an enormous receptaculum seminis which measures about 360 by 110 μ and extends from the cirrus pouch to the ovary; under high magnification its walls present a curious herring-bone pattern.

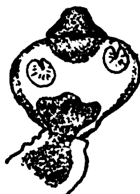


Fig. 171.—*Tylocephalum dierama.* Head, × 20. (After Shipley and Hornell.)

Posteriorly, after receiving the vitelline duct and oviduct, it turns through an angle of 180° and, running forwards, opens to the uterus at the level of the genital pore.

Shell Gland. This is situated posteriorly between the two wings of the ovary.

Vitelline Glands. At first these are situated laterally, but, as the proglottides mature, they gradually extend until they cover entirely the dorsal and ventral surfaces. As they are massive and strongly developed, they effectively obscure the anatomy of the mature segment in whole mounts. The acini are a little irregular in shape and measure about 55 by 30 μ.

Uterus. The uterus at first consists of a tube with lobulated walls running in the antero-posterior axis. Posteriorly it is not in communication with the oviduct; the latter opens into the uterus about the level of the genital pore. When mature it is a simple sac entirely filling the segment.

Eggs. The largest measure 25 μ and contain a segmenting ovum; each egg bears a long filament at both poles. They were immature.

The specimens from the intestine of *Rhynchobatus djiddensis* differed somewhat from those described above. The worms

were young, and had apparently died in an extended condition; they measure up to 4·5 cm. in length and the maximum breadth was about 560 μ. They contain only about 150 proglottides, counted under a high-power magnification. Segments 106 to 112 are about square, and succeeding ones are longer than broad; the last (not gravid) measures 1·43 mm. in length and 500 μ in breadth. The lateral margins are slightly imbricated; the genital pores are irregularly alternate and are situated in the anterior third of the lateral margin. The position of the genital pore is probably to be accounted for by the fact that the worms had been preserved in an extended position.

Head. The head measures about 230 μ in length and 240 μ in breadth; the myzorhynchus, which rests in a concavity of the posterior part of the head, is cup-shaped, and has a length of about 180 μ and a breadth of about 230 μ. The posterior part of the head has a length of about 100 μ and a breadth of about 230 μ; it bears four suckers each of which has a diameter of about 55 μ.

Neck. This is very short and measures only 200 μ in length.

No details of the muscular, excretory, and nervous systems are known.

Testes. These first appear about 9 mm. behind the head; they vary in number from about thirty to forty-five, and when fully developed each has a diameter of 70 μ.

Vas deferens. The cirrus pouch is situated anteriorly to the vagina; in the posterior segments it is a very large, squarish organ extending almost halfway across; it measures 230 by 250 μ in full development, and is situated in the anterior half of the proglottid. The cirrus is unarmed and, along with a portion of the vas deferens, lies coiled within the pouch.

Ovary. The ovary is a massive organ occupying a considerable portion of the segment posteriorly. It is composed of fine granular material apparently not divided up into acini. It stains very lightly, and thus, as in the specimens described above, contrasts strikingly with the massive, deeply-staining vitelline glands.

Vagina. The vagina passes behind the cirrus pouch and, turning backwards, runs in the middle line, dilating into a receptaculum seminis which at first is pyriform, but which later on becomes very large and oval; it lies with its long axis almost parallel to that of the segment, and when fully developed measures about 390 by 190 μ. It resembles in detail the vagina in worms of this species obtained from *Dasybatus kuhli.*

Vitelline Glands. These are very massive organs which stain deeply, and are conspicuous both in stained and unstained

specimens. They are situated on both sides and extend almost to the middle line, being interrupted on the pore side by the cirrus pouch. No vitelline glands occur on either side laterally to the ovary, but a large strip lies posteriorly to that organ. A vitelline duct arises from the posterior median extremity of the vitelline gland on each side, and these, uniting with the duct from the strip lying behind the ovary, open into the fertilization canal. The portion of vitelline gland behind the ovary was not present in specimens of this worm taken from *Dasybatus kuhli*. Shell gland apparently absent.

Uterus. In the posterior segments the uterus is rudimentary and consists of a tube with irregular lateral walls running in the antero-posterior axis.

Eggs unknown.

A number of free gravid segments apparently belonging to *T. dierama* have been found free in the gut of *Rhynchobatus djiddensis*. They measure 4 mm. in length and 1 mm. in breadth. The pore is in the anterior third of the segment. The eggs are globular and are 32 μ in diameter ; the oncosphere measures about 20 μ. and in all probability was immature.

These specimens differ from those described from *D. kuhli* above in (1) having fewer segments, some of which are longer than broad ; (2) the vitelline glands not entirely covering the dorsal and ventral surfaces, and in possessing an isolated strip of vitelline gland posteriorly to the ovary ; and (3) the genital pore being situated in the anterior third of the lateral margin.

It may be that these differences are due to the specimens from *Rhynchobatus djiddensis* being younger, and also to their having been preserved in an extended condition. The form of the head in species of this genus is subject to considerable variation.

Tylocephalum kuhli Shipley & Hornell, 1906.

" A single specimen was taken from the intestine of *Trygon kuhli*. It measured 12 mm. in length, and its greatest width, which lies a little before the posterior end, is 0·6 mm. The head consists of two portions, something like a cottage-loaf, and in general resembling those of *T. uarnak* and *T. trygonis*. The anterior part or myzorhynchus is, however, somewhat smaller than in those species. The larger and posterior part bears four small spherical suckers. The muscles which enter the head from the body spread out in this portion in a button-like manner. Immediately behind the head is a constriction, and then the proglottides begin.

" At first the proglottides are very shallow, with projecting rims like a pile of saucers upside-down, then about half-way

along the body each proglottis is seen to have a groove in it dividing it into approximately equal halves. If we trace the proglottides still further back, we see that these two halves have very different fates ; the anterior becomes the proglottis full of reproductive organs, etc., the posterior becomes the pronounced, everted, and almost recurved, salient edge.

"The hindermost proglottis is square, and in no case is the longitudinal diameter greater than the transverse. The last two or three proglottides had the penis protruded, and these were all on the same side." (*Shipley & Hornell.*)

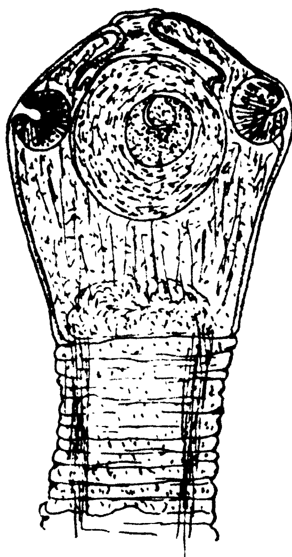


Fig. 172.—*Tylocephalum dierama.* Head, × 70. (After Jameson.)

The worm was described from a single specimen, and is ndistinguishable from *T. dierama* : it appears to the writer o be a young worm—possibly slightly abnormal—of the latter species.

Tylocephalum ludificans Jameson, 1912.

Jameson described this worm and its larval stage as follows :—"The larger globular larva ; the supposed pearl-producing worm . . . rostrum or *myzorhynchus* (Linton) retractile within a denticulated collar. Form more elongated when liberated from capsule ; length 0·5 to 1·5 mm. Average

diameter of seven specimens sectioned on Professor Herdman's slides and examined by the writer, 0·78 mm.

"Myzorhŷnchus uniformly muscular, without obvious division into muscular tracts ; retractile within annular collar ; in section it may appear either conical, lenticular, or flattened, concave and sucker-like ; protrudes as a conical papilla when in locomotion. This anterior muscular region, including the collar, is about one-third of the total length of the larva when extended. The whole myzorhynchus can be protruded, the collar then forming an annulus around it. Collar or cephalic sheath muscular with denticulated cuticle, the denticles tricuspid. . . . The denticles measure from 3 μ to 5 μ in diameter. Hinder part of the larva centrally parenchymatous, the

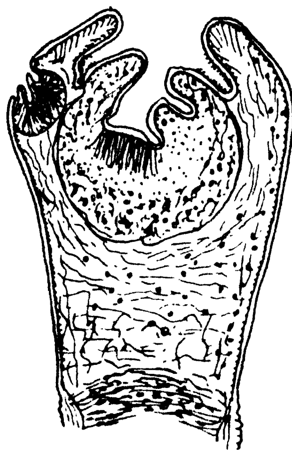


Fig. 173.—*Tylocephalum dierama*. Horizontal section of head. × 70. (After Jameson.)

parenchyma containing the calcareous corpuscles characteristic of Cestode larvæ, peripherally more muscular. The hinder part of the body is covered by a thick, radially marked epicuticle permeated by numerous closely-set tubuli, and suggesting on superficial examination a coat of cilia. This epicuticle varies in thickness but is generally about 0·03 mm. thick, and the true cuticle lies under it.

"This form is distinguished from *Tylocephalum minus* by its larger size (Herdman gives the size as about six times that of the smaller form), the undivided musculature of the myzorhynchus, and the wider and more open character of the collar-sheath of the myzorhynchus in the resting-stage.

Habit:—Resting in spherical fibrous cysts, derived from the connective tissue of the host, in the Ceylon Pearl Oyster, *Margaritifera vulgaris*. Most frequent in the visceral mass, notably the liver. *Habitat*:—Gulf of Manaar (Herdman and Hornell). Trincomalee (Willey).

"The following description is of a worm which I regard as in all probability the adult of this larva. The single specimen was obtained from the spiral intestine of *Ætobatis narinari*, by Mr. Hornell, on 4th January, 1905, and had apparently been overlooked by Mr. Shipley among some duplicate specimens of *Kystocephalus translucens*, along with which I found it when examining Dr. Shipley's material. After it had been cleared and examined as a transparent object, Dr. Shipley very kindly allowed me to have sections cut from it to compare with those of the larva in the pearl oyster."

? Adult of *Tylocephalum ludificans* Jameson, 1912.

From *Stoasodon narinari*, Pearl Banks, Ceylon.

"Length, 12 mm. Head, 0·6 mm. long by 0·5 mm. broad; pyriform, slightly broader in front than behind: transition from head to neck not very sharply defined. The myzorhynchus in this specimen is retracted within its sheath, as is usually the case with the larva in the pearl oyster; it is about 0·3 mm. in diameter. Around the head are four marginal suckers about 0·125 mm. in diameter. Proglottides about 40 in number, increasing but little in breadth from before backwards; they begin to increase notably in length from about the eighty-fifth backwards. The largest hindermost segments are about 0·5 mm. long, and slightly longer than broad. The armature of the collar is similar to that of the larva. In section the myzorhynchus is seen to be retracted in such a way that its anterior surface is thrown into folds. . . . The only point in which the head of this worm appears to differ from the larva in the pearl-oyster is in the presence of the four marginal suckers, which may well be a feature first acquired in the final host."

Unfortunately it is impossible to identify this parasite from the above description, as the genital organs are not described, and it is not known whether the worm was gravid, or fully or partly mature; but Jameson's figure of the head and the adult leaves little room for doubt, in the writer's opinion, that his mature form is identical with *Tylocephalum dierama* Shipley & Hornell. It is not established that the larva described by Jameson as that of *T. ludificans* actually belongs to the adult of that name. It may, in fact, belong to any species of *Tylocephalum*. The same larva was believed by Herdman to be the young of *Tetrarhynchus unionifactor*,

around which orient pearls were formed in the Ceylon pearl oyster *; it is exactly like the head of an adult *Tylocephalum*, except that the suckers have not developed, but it is obviously impossible to say at the present time to which species it belongs.

(3) **Tylocephalum translucens** (Shipley & Hornell, 1906). (Fig. 174.)

Synonym :—*Kystocephalus translucens* Shipley & Hornell, 1906.

From *Stoasodon narinari*, Pearl Banks, Ceylon. Hornell.

The description of the genus *Kystocephalus* was as follows :—" Head bladder-like, with four small suckers and a myzorhyn-

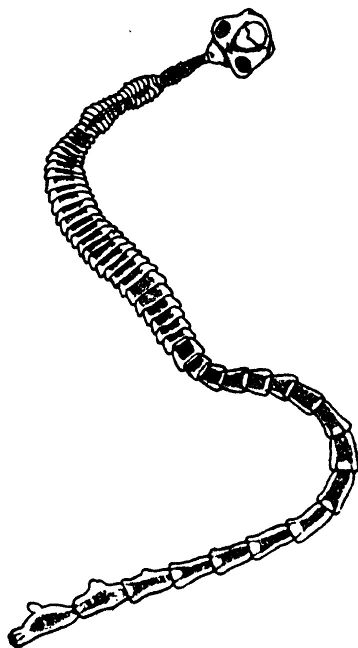


Fig. 174.—*Tylocephalum translucens.* Entire worm, × 16. (After Shipley and Hornell.)

chus which is partially covered by a membrane. Proglottides with very salient posterior borders, most of them much broader than long. Lips of reproductive pores, which are irregularly alternate, very prominent." (*Shipley & Hornell.*)

* What Shipley and Hornell believed to be the adult of this larval form occurred in *Rhinoptera javanica*, and is undoubtedly a tetrarhynchid.

Shipley and Hornell described *K. translucens* as follows :—"The two specimens of this worm at our disposal measured, respectively, 10 mm. and 35 mm., yet each appeared to end in ripe proglottides. The head and the thicker part of the body measured 0·4 mm. in breadth. The head is a curiously bladder-like concern which takes little stain and bears four very small spherical suckers. There seems to be a myzorhynchus, surrounded, and half enclosed in, a circular membrane. The membrane, however, has a central circular aperture through which the myzorhynchus protrudes. Immediately behind the head the proglottides appear and for about one-half the body-length they are considerably broader than long; they then become square, and the last five or six are longer than broad. The posterior end of each proglottis widens out like the walls of a funnel and overlaps the anterior end of the succeeding proglottis to a much greater extent than is usual, so as sometimes to cover a third of the hinder proglottis. At least this is the case in one of our specimens; in the other, this salient edge was curled back like the brim of a top hat. The genital orifices are lateral and in the posterior proglottides have very prominent lips; they are irregularly alternate, usually two or three on one side and then three or four on the other. This form seems to be not far removed from the genera *Tylocephalum* and *Cephalobothrium*, but is marked off by quite definite features."

The genus is indistinguishable from *Tylocephalum*.

The species *Tylocephalum translucens* (Shipley and Hornell) appears to be quite distinct. It resembles *T. dierama* in the segments having salient lateral posterior margins, but it differs from it in the possession of an enormous genital pore. It is similar to *T. uarnak* in possessing a large pore, but appears to differ from it in having a relatively larger head and in the lateral margins of the segments being strikingly salient. The anatomy of the species is not known.

(4) **Tylocephalum uarnak** Shipley & Hornell, 1906. (Figs. 175 & 176.)

From *Dasybatus uarnak*, *D. walga*, and *D. kuhli*, Pearl Banks, Ceylon. Hornell; Southwell.

According to Shipley and Hornell, this worm, of which they had "a few examples," measured 3·5 cm. in length and consisted of from thirty to forty segments. The greatest breadth of the body was 700 μ. The head consisted of an anterior lobe resting on a square cushion, which latter bears a sucker at each angle. There is a short neck. The authors state that the "excretory pore is immense, a great round opening more or less median." (Probably this remark applies

to the genital pore, which is enormous.) The testes are scattered mostly at the anterior end of the proglottid, and, as the uterus develops, they are pushed towards the periphery. The uterus is a long sac constricted in the middle. The posterior segment measures at least 5 mm. in length, and some segments are ten times as long as they are broad; none of them overlap. The worms vary within wide limits in the number of segments in the strobila, the number of testes in a segment, and the size of the head.

In the following table a comparison is made between *T. uarnak* and the closely related species *T. minutum* Southwell, 1925:—

	Tylocephalum uarnak.	*Tylocephalum minutum.*
Length of worm	8 mm. to 3 cm.	2 cm.
Breadth of worm	145 to 400 μ	680 μ
Number of segments....	20 to 87	11 to 20, usually 16.
Number of testes	16 to 27	38 to 63, usually about 40.
Length of head	About 220 to 280 μ.	530 μ
Breadth of head	210 to 410 μ	440 μ
Length of myzorhynchus	125 to 210 μ	260 μ
Length of posterior part of head.	110 to 140 μ	270 μ
Length of last segment..	850 to 2·12 mm.	4·5 mm.
Eggs	Few (about 150) per segment.	More numerous.

The edges of the proglottides are straight and their posterior lateral margins are not salient. The genital pore occurs in the posterior third of the segment; at first it is situated on the mid-ventral line, but, as the worm becomes gravid, it is displaced laterally. The pore is enormous and is surrounded by a sucker whose margins are produced into a frill; it leads into a genital atrium very similar to that described for *T. trygonis*. The position of the genital organs varies according to the number of segments composing the worm.

Head. The head, which measures from about 220 to 280 μ in length and from 210 to 410 μ in breadth, resembles that of *T. trygonis* and *T. pingue*. The anterior myzorhynchus is from 125 to 260 μ in length and is armed with innumerable small spines which measure about 6 to 9 μ in length; these, however, are frequently lost. The posterior part bears four suckers and is from about 100 to 270 μ in length. The diameter of the suckers is about 70 μ.

Neck. This is very short, being only from 140 to 160 μ in length.

The muscular system resembles that described for *T. trygonis*.

Testes. The testes vary in number from about sixteen to twenty-seven; when fully mature each has a diameter of about 45 μ, and they are arranged like an inverted U on each side of the middle line in the anterior half of the segment. They do not appear until the ovary is mature; they persist even after the uterus is fully developed, and can frequently be seen in the penultimate proglottid.

Vas deferens. The first indication of the genital pore consists, anteriorly, of a pronounced condensation of dense granular tissue in the centre of the segment. More posteriorly the pore arises in the centre of this mass and opens on the ventral surface. In the last six or seven segments the pore becomes situated laterally in the posterior third of the pro-

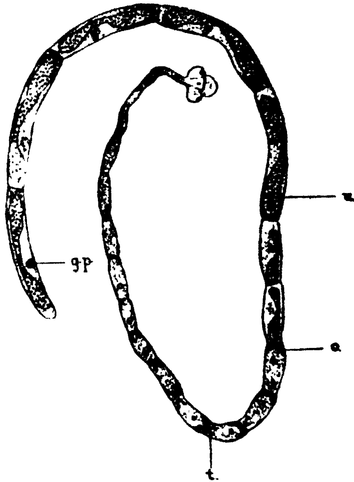


Fig. 175.—*Tylocephalum uarnak.* Entire worm, × 18. (After Southwell.)

glottid. It is surrounded, in the gravid segment, by a sucker having a scalloped frill, not quite so prominent as that described for *T. trygonis*. The pore leads into a large genital atrium whose walls are glandular; at the base of the atrium the openings of the cirrus pouch and vagina can be seen, the latter lying posterior to the former. The cirrus pouch is peculiar in that it lies in the median line, its long axis being parallel to that of the segment. It appears late, and only attains its full development in gravid proglottides. The cirrus is dilated, unarmed, and almost straight, opening, as noted above, at the base of the genital atrium. The pore is surrounded by a strongly developed sphincter muscle. The

cirrus appears to occupy the whole of the pouch. Outside the latter the vas deferens is a long stout tube running anteriorly in the middle line. External seminal vesicle absent; the internal vesicle consists of a club-shaped dilatation on the median portion of the cirrus.

Ovary. The ovary is a massive, somewhat bilobed organ situated posteriorly and extending about two-thirds the distance between the posterior margin of the proglottid and the

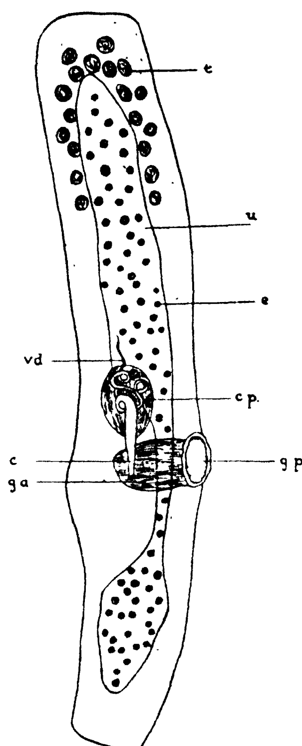


Fig. 176.—*Tylocephalum uarnak*. Nearly gravid segment, × 13. (After Southwell.)

genital pore; it is only to be seen in about five segments, and disappears quite suddenly; it is composed of rather large acini densely crowded together.

Vagina. The vagina opens at the base of the genital atrium, the opening being posterior to that of the vas deferens; it is a very short tube running directly from the pore to the anterior part of the centre of the ovary, where it dilates into a very large receptaculum seminis.

Vitelline Gland. This is a small organ, either round or bilobed, situated posteriorly to the ovary ; a duct arises from each lateral anterior margin, and these, uniting together, open into the oviduct.

Shell Gland. A granular organ, globular in shape, about 40 μ in diameter, surrounding the fertilization canal.

Uterus. Resembles exactly that described for *T. trygonis.*

Eggs. The uterus contains very few eggs ; no mature ones were seen ; the largest measured about 60 μ and the segmenting ovum 24 μ.

This species is very similar to *T. trygonis*, but differs in having (1) the genital pore situated on the ventral surface in the anterior two-thirds of the segment ; (2) a larger number of testes ; and (3) the long axis of the cirrus pouch situated in the antero-posterior axis of the segment.

(5) **Tylocephalum minutum** Southwell, 1925.

From *Urogymnus* sp. (*? asperrimus*), Pearl Banks, Ceylon. Southwell.

This species resembles *T. uarnak* very closely ; it differs from it in having fewer segments, a larger number of testes, and in the vitelline glands extending along the lateral margins. A comparison between the two species is given on p. 322.

(6) **Tylocephalum yorkei** Southwell, 1925. (Figs. 177, 178, & 179.)

From *Stoasodon narinari*, Puri, Orissa, India. Southwell.

The worms measure at least 8 cm. in length, and the maximum breadth is about 700 μ. They are oval in cross-section and are composed of several hundred segments having very salient posterior lateral margins. These are at first broader than long ; they become square as the testes begin to mature. The largest posterior one in the writer's specimens measured 750 μ in length and 600 μ in breadth ; it was not gravid. The genital pores are irregularly alternate and are situated just a little behind the middle of the lateral margin.

Head. This resembles those of *T. trygonis*, *T. uarnak*, and *T. pingue*, but in *T. yorkei* the myzorhynchus is larger, more flattened, and armed with innumerable spines which measure from 15 to 17 μ in length. Occasionally the anterior central part of the myzorhynchus is marked by a deep fossa bordered by thick lips. The head proper is somewhat cushion-shaped and bears four suckers ; its length, including the myzorhynchus, varies from 400 to 500 μ, and its breadth from 550 to 700 μ.

Neck. The neck is very short, measuring only 90 to 100 μ in length.

Muscular System. Immediately beneath the cuticle there is a layer of subcuticular muscles. Oblique fibres are somewhat scanty and lie embedded in the parenchyma, which is strongly developed. The principal muscles consist of a series of large, longitudinal bundles arranged parallel to the cuticle in a single layer, the bundles being well separated from each other. External to them are a number of very small and irregularly disposed fibres. Internally to the larger bundles, and separated from them by parenchyma, there are a few circular muscles. After the testes are almost fully developed the musculature atrophies. In the neck the longitudinal fibres converge into a few bundles, and these, running to the head, spread out fanwise in the myzorhynchus. A few also run to each sucker.

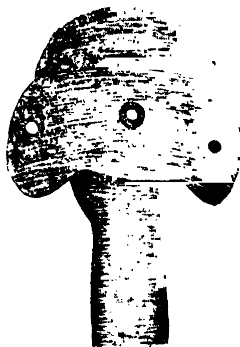


Fig. 177.—*Tylocephalum yorkei.* Head, × 56. (After Southwell.)

Excretory System. There are a pair of vessels along each lateral margin; they are of equal calibre, and the genital ducts run between them.

Nervous System. There is a single nerve running along each lateral margin externally to the two water vessels.

Testes. The testes vary in number from twenty-six to thirty, and appear about 2 mm. behind the head. At first they are arranged in the form of a ring in the centre of the segment, and in this condition they occupy sixty or seventy proglottides gradually increasing in size. When mature they fill the entire segment, and each testis is oval and measures about 110 by 75 μ.

Vas deferens. The cirrus pouch lies dorsally to the vagina and extends about one-quarter the distance across the segment; it does not reach its full development until the ovary is well

formed, and even then it is somewhat inconspicuous; the cirrus is slightly swollen and unarmed; a few coils of the vas deferens lie within the pouch. Outside this organ it is short and coiled, and lies in the antero-posterior plane in front of the cirrus pouch. Seminal vesicle absent (?).

Ovary. The ovary is small, bilobed, and situated quite posteriorly; each lobe consists of a number of very long cylindrical acini radiating laterally from the centre of the posterior margin of the segment.

Vagina. From the pore the vagina runs anteriorly and parallel to the cirrus pouch and between the dorsal and ventral excretory vessels. At the median extremity of the cirrus

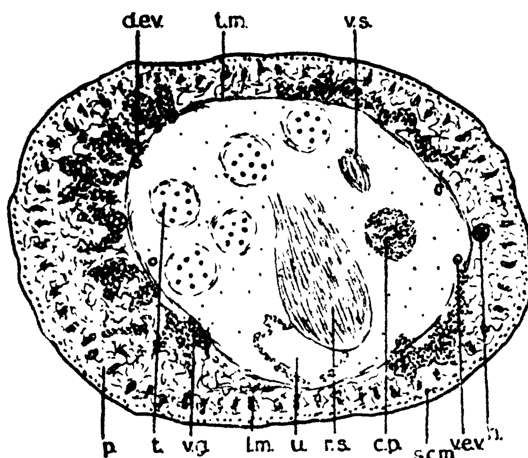


Fig. 178.—*Tylocephalum yorkei*. Transverse section of mature segment, × 112. (After Southwell.)

pouch it turns posteriorly and runs as a short duct to a very large receptaculum seminis. Behind this organ the uterus arises, and the vagina, continuing posteriorly, receives the ducts from the vitelline and shell glands. It then curves forwards and continues as the oviduct, opening to the uterus at a point opposite the genital pore.

Shell Gland. This is a small organ situated close to the opening of the vitelline duct, *i.e.*, just where the vagina, curving anteriorly, continues as the oviduct. It has a diameter of about 40 μ.

Vitelline Glands. The vitelline glands consist of a number of acini situated along each lateral margin and extending the whole length of the segment. At first the acini are disposed in single file, but in full development this arrangement is lost. The long axis of each acinus lies parallel to the transverse

axis of the segment. When fully developed, each unit measures about 60 by 30 μ, and, being crowded together, they appear as a dense mass.

Uterus. The uterus arises before the testes are fully developed, and consists of a central stem, with lobular walls, extending in the antero-posterior axis of the segment. When the testes are fully developed it is frequently pushed towards one of the lateral margins. Posteriorly it is blind and is not in communication with the oviduct or fertilization canal. The oviduct is a rather long tube opening to the uterus at a point

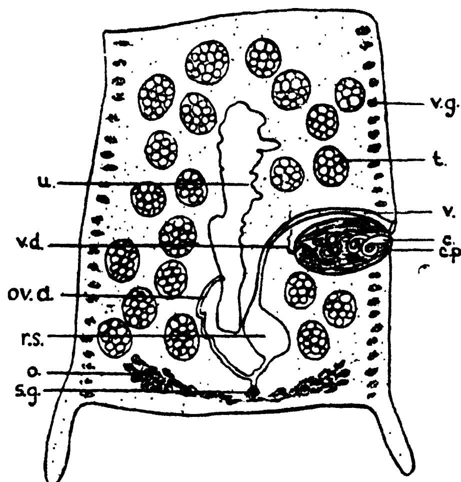


Fig. 179.—*Tylocephalum yorkei.* Horizontal section of mature segment, × 334. (After Southwell.)

nearly opposite the genital pore. In this respect the worm resembles *Acanthobothrium coronatum*, *A. uncinatum* (Zschokke), *Calliobothrium leuckarti*, and *C. verticillatum*.

Eggs unknown.

SPECIES INQUIRENDÆ.

(7) **Tylocephalum ætobatidis** (Shipley & Hornell, 1905) Shipley & Hornell, 1906.

Synonym :—*Tetragonocephalum ætiobatidis* Shipley & Hornell, 1905.

From *Stoasodon narinari* and *Dasybatus walga*, Pearl Banks, Ceylon. Hornell.

The authors gave the following description of this species :—" A single specimen of another Cestode . . . was found . . . in *Ætiobatis narinari*. Its length was 1·3 cm., and its breadth, which was remarkably uniform behind the head, was 0·5 mm. The head was three times this breadth and consisted of a

rostellum, long and conspicuous and unarmed, and with a swollen base, squarish in cross-section, with four small suckers at the anterior angles. Posteriorly the basal portion overlapped the anterior proglottides. There is no neck, but the proglottides appear immediately after the head, at first very narrow but with marked constrictions; as they increase in size the posterior angle becomes salient. . . . The last three proglottides are twice the length of those which immediately precede them and this growth is somewhat sudden. The head, though it differs greatly in its proportions, resembles in essentials the head of *T. trygonis*. The marked saliency of the posterior edge of the proglottides separates off the species in question from the species which inhabits *Trygon walga*. As there was but a single specimen, it did not seem advisable to cut it, and as it was preserved in osmic it was not possible to make out anything of the internal anatomy."

The definition of their genus *Tetragonocephalum* was as follows:—" Head unarmed, consisting of an anterior knob-like portion arising from a cubical base; the four posterior corners of the cubical base having minute suckers, each with a papilla."

(8) **Tylocephalum minus** Jameson, 1912.

From the pearl oyster (*Margaritifera vulgaris*), Pearl Banks, Ceylon. Herdman.

" (The smaller globular larva, which Professor Herdman thinks may also be concerned in pearl formation, *Tetrarhynchus* sp., Herdman.) . . . .

" Diameter of resting parasite in cyst from 0·07 to 0·2 mm. Average diameter of forty examples shown on Professor Herdman's slides and measured by the present writer, 0·14 mm. Body sub-globular, consisting, as in *T. ludificans*, of an anterior muscular and a posterior parenchymatous part, the anterior muscular portion (myzorhynchus) consisting of a conical papilla in a cup or flask-shaped depression formed by the surrounding muscular collar or sheath. As a rule, in preserved specimens, the opening of this depression seems relatively narrower, and the papilla more conical and less flattened than in the previous species. The musculature of the myzorhynchus shows, in some examples, a tendency to break up into four longitudinal tracts. In young examples the myzorhynchus may be barely differentiated. Cuticular spines are present on the collar, but they are smaller and relatively finer than in *T. ludificans*. The epicuticle is about 0·01 mm. thick.

" This form is distinguished from *T. ludificans* by its smaller size and finer armature of the collar, and by the tendency of the myzorhynchus musculature to break up into four strands. It is regarded by Southwell as the same species as *T. ludificans*.

" Professor Herdman, while he regards the form here named *T. ludificans* as the pearl producer *par excellence*, considers that the present species too 'may occasionally form the nuclei of pearls' (Report V, p. 22). Particulars of the structure of both these forms are given on pp. 79-82 of Part II of Professor Herdman's Report." (*Jameson.*)

As this worm was described from larval forms, the adult is not known, and it is quite probable that, when the life history is established, it will be found to be a species of *Tylocephalum* already described.

Genus IV. ADELOBOTHRIUM Shipley, 1900.

Shipley described this genus as follows :—" Head with rostellum embedded in tissues of host, but bearing no hooks. Behind the head the neck swells out into an enormous ruff-like collar. This bears, on its anterior face, four very small suckers which seem to take little or no part in the attachment of the worm to its host. The section of the body anteriorly is circular, and so is that of the anterior end of each proglottis, but the ripe proglottides tend to be flattened in their middle region. Each proglottis is produced backwards into a very prominent ridge which ensheaths the succeeding proglottis to a varying extent according to their age. The genital pores are unilateral and irregular [*sic*], but groups of three openings on one side, followed by groups of three openings on the other, succeed one another with some regularity, in certain regions. Both dorsal and ventral longitudinal water-vascular canals persist and, anteriorly, the longitudinal muscles are in unusually powerful and distinct bundles." Type species :— *Adelobothrium œtiobatidis* Shipley, 1900.

The genus is closely related to *Tylocephalum*, from which it differs in having the posterior part of the head membranous and collar-like, instead of subglobular and solid. It differs from *Balanobothrium* in having the suckers on the posterior, instead of the anterior, part of the head, and in the absence of hooks.

Adelobothrium ætobatidis Shipley, 1900. (Figs. 180, 181, 182, 183, & 184.)

Synonym :—*Tylocephalum marsupium* Linton, 1916.

From *Rhynchobatus djiddensis*, Pearl Banks, Ceylon. Southwell.

Shipley states that this species measures about 4 to 5 cm. in length and has a breadth of 1·5 mm. ; the testes are large and scattered evenly through the proglottid. The cirrus is

unarmed. The ovary is posterior, and close to it is a finger-shaped shell gland. The lateral vitelline glands are prominent, and their tubules unite to form a wide canal which, with the similar one from the other side of the body, opens into the duct which leads from the ovary into the uterus. The latter is figured arising immediately in front of the ovary, running in the antero-posterior axis, as a tube with lobulated walls. The worms, which are composed of over two hundred segments, measure up to 8 cm. in length, and they have a maximum breadth of about 1·5 mm. The entire strobila is circular in cross-section. At first the segments are broader

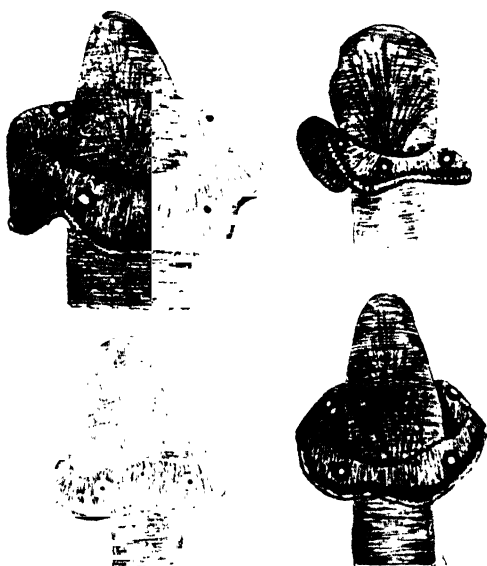


Fig. 180.—*Adelobothrium ætobatidis*. Views of the head, × 35. (After Southwell.)

than long, but the gravid terminal ones are longer than broad, the largest measuring about 1·3 mm. in length and 750 μ in breadth. The posterior lateral margins only are salient (imbricated). The genital pores are irregularly alternate, and are situated about the middle of the lateral margin. There is no neck.

Head. The entire head measures about 1·2 mm. in length, and it has a maximum breadth of about 220 μ. Anteriorly there is a large myzorhynchus, 850 μ in length, which is usually conical in shape, with a rounded anterior extremity.

Even in very young worms it is not covered with spines, but its posterior part is covered with an immense number of extremely minute rugosities which, under the oil immersion, have the appearance of very fine down or cilia, but no spines could be discovered. The posterior part of the head

Fig. 181.

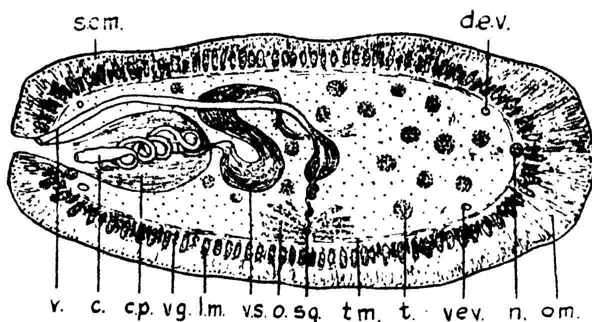
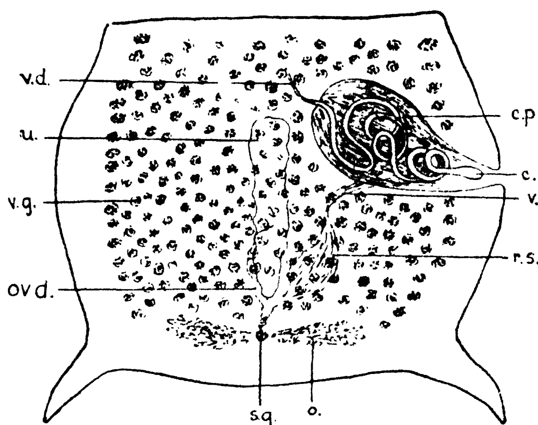


Fig. 182.



Adelobothrium ætobatidis.

Fig. 181.—Transverse section of mature segment, × 75. (After Southwell.)
Fig. 182.—Mature segment, × 75. (After Southwell.)

consists of a membranous collar bearing four suckers very similar to that of *Balanobothrium tenax*.

Muscular System. This is well developed; immediately beneath the cuticle there is a layer of subcutaneous muscles. Dorso-ventral fibres are fairly numerous and are well seen in

transverse sections. There is a ring of large bundles running parallel with the cuticle, and internal to this a few annular fibres can be seen.

Excretory System. There are two vessels of equal size running along each lateral margin. The vagina and cirrus pouch run between them.

Nervous System. There is a single nerve lying external to the excretory vessels on each side.

Testes. The testes vary in number from about 130 to 150, of which about twenty-five are situated posteriorly to the cirrus pouch on the pore side. When fully developed they occupy practically the whole of the segment; they are somewhat oval and each measures about 55 by 45 μ.

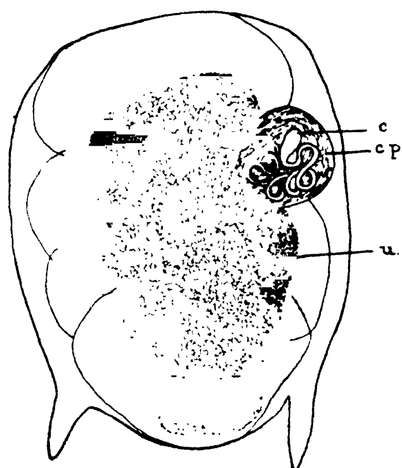


Fig. 183.—*Adelobothrium ætobatidis.* Gravid segment, × 47. (After Southwell.)

Vas deferens. The cirrus pouch, when fully developed, measures about 320 μ in length by about 200 μ in breadth. It passes between the two water vessels and dorsally to the vagina; the cirrus is unarmed and extremely long; when not protruded it forms numerous coils within the cirrus pouch. In many segments it was protruded and measured over 1·4 mm. in length. being as long as three segments. Outside the pouch the vas deferens dilates anteriorly to the cirrus pouch and quite close to the lateral margin into a long and wide muscular seminal vesicle which is loosely coiled. The terminal part of the vas deferens lies anteriorly in the antero-posterior axis.

Ovary. The ovary is bilobed and situated posteriorly, and, even when fully developed, it is very narrow antero-posteriorly. It consists of a number of oval or cylindrical acini.

Vagina. From the pore the vagina runs ventrally to the cirrus pouch. At the median extremity of the latter organ it turns backwards and almost immediately dilates into an enormous muscular receptaculum which, when fully developed, occupies a considerable portion of the area between the cirrus pouch and the ovary; it is not figured by Shipley. Posteriorly to the receptaculum the vagina narrows and immediately behind the origin of the uterus it receives the common vitelline duct and then continues as the oviduct.

Shell Gland. This is a globular organ, measuring about 90 by 60 μ, situated between the two lobes of the ovary, and apparently disposed round the oviduct.

Vitelline Glands. These glands are very conspicuous, and

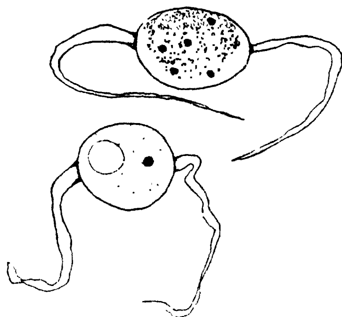


Fig. 184.—*Adelobothrium ætobatidis.* Eggs, × 600. (After Southwell.)

consist of very large isolated acini. In young proglottides they only occur along each lateral margin, but, as the segment becomes ripe, the glands extend until they cover the entire dorsal and ventral surfaces. The common duct opens to the fertilization canal just posteriorly to the origin of the uterus.

Uterus. This arises as a tube with lobulated walls running forwards from the centre of the ovary in the antero-posterior axis. It continues to develop as a simple sac, and ultimately fills the segment entirely; the seminal vesicle and the receptaculum seminis are then pushed to the lateral margin.

Eggs. These are round or slightly oval, and bear a long filament at each pole. They measure about 25 μ in diameter, and the filaments each measure up to 80 μ in length. Ripe eggs have not been seen.

Genus V. BALANOBOTHRIUM Hornell, 1912, emended.

Scolex acorn-shaped, consisting of a bulbous head bearing four suckers and armed with simple or compound hooks; surrounding the posterior part of the head is a collar-like pseudoscolex.

Hornell's definition of the genus was as follows :—" Scolex acorn-shaped, consisting of a bulbous head surrounded at the base by a cup-shaped membranous collar; a pair of very minute two-pronged uncini situated at four equidistant points on the upper circumference of the head, a minute acetabulum above each pair of uncini. Neck extremely short. Strobila ligulate, the proglottides short and wide."

Type-species :—*Balanobothrium tenax* Hornell, 1912.

Key to Species.

Small worms up to 3·5 cm. in length, with less than 200 testes	*B. parvum*, p. 339.
Large worms up to 35 cm. in length, with over 500 testes	*B. tenax*, p. 335.

(1) **Balanobothrium tenax** Hornell, 1912. (Figs. 185, 186, 187, & 188.)

From (1) *Stegostoma tigrinum*, Bay of Bengal and Pearl Banks, Ceylon. Hornell. (2) *Dasybatus walga*, Pearl Banks, Ceylon. Southwell.

Hornell gave the following diagnosis of his species :— " Scolex consisting of a bulbous sub-conical head encircled at the base by a cup-like bothridial collar. Four pairs of minute two-pronged uncini disposed at equal intervals around the circumference of the head-bulb; the prongs are sharply bent at mid-length and borne upon a common horizontal bar; in young specimens a spur-shaped projection occurs opposite the base of the outer and longer prong. No definite neck. Strobila ligulate, long and stout, 33 cm. in dead condition. Narrow at anterior end, 1·3 mm., increasing slowly and uniformly in width till it attains 4 mm. in front of the region of ripening proglottides. Proglottides short, five to six times broader than long in the wide region posterior to mid-length; ripe proglottides characteristically short and length never greater than breadth. Grooves of segmentation apparent immediately behind bothridial collar. Cuticle striated transversely, with minute furrows. Ovaries arranged centrally in a rosette of large pear-shaped globules. Genital pores lateral, opening well forward and anterior to mid-length; disposition irregular, in alternative consecutive series of from two to six on the same side."

Hornell drew attention to the fact that in life the bulbous portion of the head is embedded in a sac like outgrowth from the internal wall of the gut. This outgrowth hangs freely in the cavity of the intestine and has its base greatly constricted. The mouth or apex of the outgrowth is extremely small and tightly encircles the narrow region of the head of the worm situated between the scolex proper and the collar. In order to see the head properly this sheath has to be removed.

The worms vary in length up to about 33 cm.. and consist of a large number of segments. The greatest breadth is about 4·5 mm.; the last segment measured 4 mm. in breadth

Fig. 185.

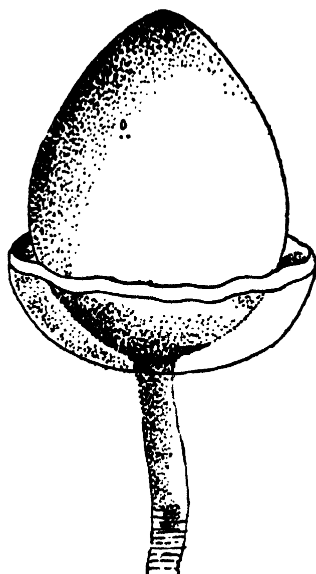


Fig. 186.



Balanobothrium tenax.

Fig. 185.—Head, × 16 (note minute suckers and hooks). (After Southwell.)
Fig. 186.—A pair of hooks. (After Southwell.)

and 2·5 mm. in length. The genital pores are irregularly alternate and are situated a little in front of the middle of the lateral margin. The uterine pore is prominent and is placed at the middle of the ventral surface.

Head. The bulbous subconical head measures about 2·7 mm. in length and 2·2 mm. in breadth. The collar or pseudoscolex has a length of about 600 μ and a breadth of about 2 mm. There are four extremely minute suckers on the bulbous portion of the head situated equidistant from each

other. They have a diameter of about 40 to 50 μ only. Beneath, or posterior to, each sucker there are a pair of compound hooks, the measurements of which are as follows :—Length of basal part, 28 to 32 μ; breadth, 14 μ; length of larger prong, including base, 32 μ; excluding base, 18 μ; length of smaller prong, including base, 23 μ; excluding base, 12 μ.

Neck. The neck is very short, measuring only about 3 to 4 mm. in length.

Muscular System. Immediately beneath the cuticle there is a layer of subcuticular fibres. The oblique fibres are fairly prominent, and run between the bundles of longitudinal muscles. The latter are strongly developed and consist of a number of large internal bundles, together with numerous others, which decrease in size towards the external surfaces; all these fibres are distributed in a single layer. Internally to the longitudinal muscles there is an annular layer.

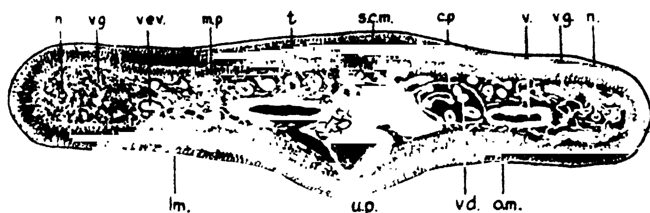


Fig. 187.—*Balanobothrium tenax.* Transverse section of mature segment, × 28. (After Southwell.)

Excretory System. There is a large ventral excretory vessel, having a diameter of about 150 μ, near each lateral margin. The dorsal vessel is so small that it can only occasionally be seen even under high-power magnifications; it has a diameter of about 5 μ only. The cirrus pouch and vagina run dorsally to the ventral vessel.

Nervous System. There is a single nerve situated laterally to the excretory system.

Testes. There are over 500 globular testes; when fully developed they each measure about 60 μ in diameter. They are situated dorsally; on the pore side there are about 130 behind and about 110 in front of the cirrus pouch. In the aporal half of the segment there are about 300.

Vas deferens. The cirrus pouch lies posteriorly to the vagina and has a length of about 900 μ and a breadth of about 300 μ. The cirrus is densely beset with very minute spines or hairs. A number of coils of the vas deferens lie inside the pouch. Outside the latter it is thrown into a number of coils which

extend almost to the middle of the segment and slightly in front of it. Seminal vesicle absent.

Ovary. The ovary consists of two wings situated quite posteriorly; each half consists of a number of elongated club-shaped lobes radiating laterally, and each is densely granular in appearance. In Hornell's figure the uterus is shown as the ovary.

Vagina. From the pore the vagina runs in front of the cirrus pouch. At the median extremity of the latter it bends at right angles and turns backwards to the centre of the ovary, where it becomes confluent with the oviduct and receives the ducts of the vitelline glands and shell gland. At this point the uterus arises and extends forwards. Receptaculum absent.

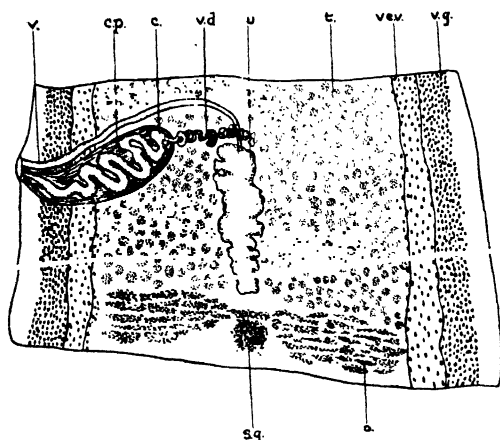


Fig. 188.—*Balanobothrium tenax*. Mature segment, × 28. (After Southwell.)

Shell Gland. This is a small organ lying posteriorly to the centre of the ovary.

Vitelline Glands. These are conspicuous organs disposed laterally to the ventral water vessels on each side and extending the entire length of the segment except where interrupted by the cirrus pouch and vagina; each acinus has a diameter of about 18 μ.

Uterus. The uterus arises in front of the ovary and runs anteriorly; at first it consists of a central stem with lobulated lateral and anterior walls. Even before it contains eggs it opens on the ventral surface by a large pore. There can be no doubt that this pore is primary and not due to dehiscence of the uterine or body wall. In full development the central uterine stem contracts and the lobuli become enlarged, giving the uterus a rosette appearance.

Eggs. No ripe eggs have been seen; those taken from the most mature segment have a diameter of 28 μ and contain a segmenting ovum, the oncosphere not having developed.

(2) **Balanobothrium parvum** Southwell, 1925. (Figs. 189, 190, 191, & 192.)

From *Dasybatus* sp. and *Galeocerdo arcticus*, Pearl Banks, Ceylon. Southwell.

The worm varies in length from about 1·6 to 3·5 cm. and the breadth from 480 μ to 1 mm.; the larger specimens are composed of about three hundred segments. At first these are very shallow, but the posterior ones are much longer than broad; the largest measured 1·6 mm. in length and

Fig. 189.

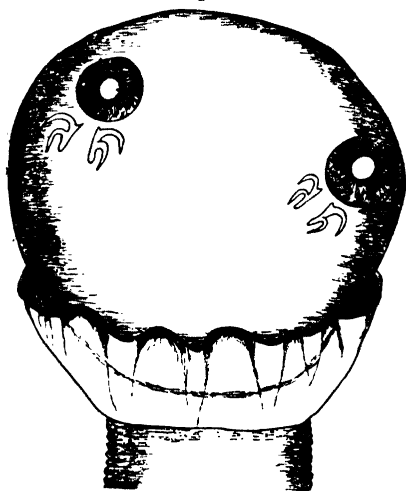
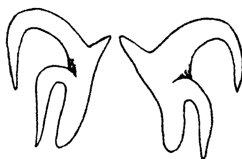


Fig. 190.



Balanobothrium parvum. (After Southwell.)
Fig. 189.—Head, × 166.
Fig. 190.—A pair of hooks, × 575.

300 μ in breadth; the lateral margins of the segments are not imbricated. The genital pores are irregularly alternate and are situated a little in front of the centre of the lateral margin.

Head. The head resembles that of *B. tenax*, but it is much smaller; it measures from 210 to 250 μ in length and from 200 to 280 μ in breadth. It consists of an anterior globular portion which bears four suckers and four pairs of compound hooks, and a posterior membranous, collar-like part; the length of the basal portion of the hook is about 31 μ,

and the distance from, and including, the basal portion to the top of the curved hook is 24 μ.

Neck. The neck measures about 1·6 mm. in length and is usually cylindrical.

Muscular System. The cuticle has a breadth of about 9 μ; immediately beneath it is a layer of longitudinal bundles having a thickness, in the vicinity of the testes, of about 110 μ. Interspersed between the bundles are a very few oblique and internally to them some annular fibres.

Excretory System. There are two vessels of about the same size on each side, one being directly dorsal to the other.

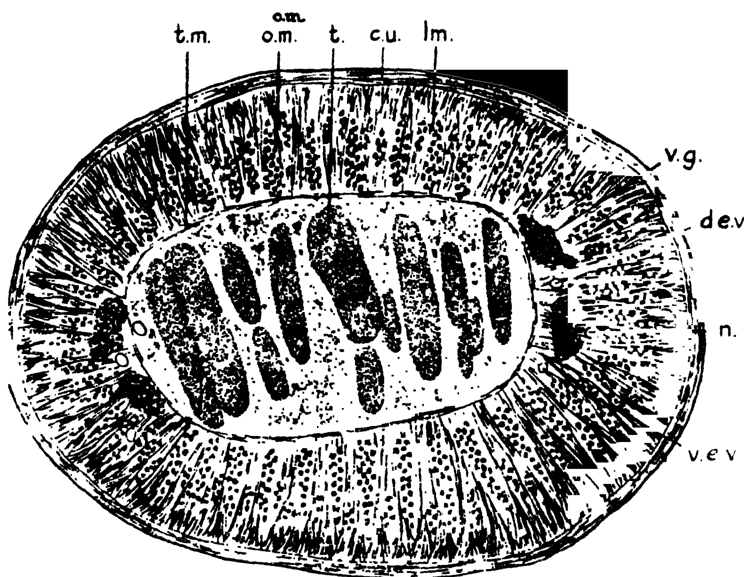


Fig. 191.—*Balanobothrium parvum.* Transverse section of an almost mature segment, × 212. (After Southwell.)

Nervous System. A single nerve runs along each lateral margin externally to the two excretory vessels.

Testes. The testes vary in number from about 110 to 140. When fully mature they are globular, and each has a diameter of 36 μ.

Vas deferens. The cirrus pouch is situated posteriorly to the vagina; the cirrus is beset with innumerable small spines, and its terminal portion is dilated. A number of coils of the vas deferens lie within the pouch. Outside the latter the vas deferens runs anteriorly from it as a much-coiled tube in the antero-posterior axis. Seminal vesicle apparently absent.

Ovary. This is situated posteriorly, and is either bilobed, U-shaped, or Y-shaped. It consists of a large number of globular acini each having a diameter of about 20 μ.

Vagina. From the pore the vagina runs in front of the cirrus pouch ; at the median extremity of the latter organ it turns backwards rather suddenly through 90° to the ovary. In mature segments the whole length of the vagina between the cirrus pouch and the ovary is very dilated and its walls are lobulated, the entire swelling acting as a receptaculum seminis.

Vitelline Glands. These consist of a single row of acini situated along each lateral margin, but at the posterior

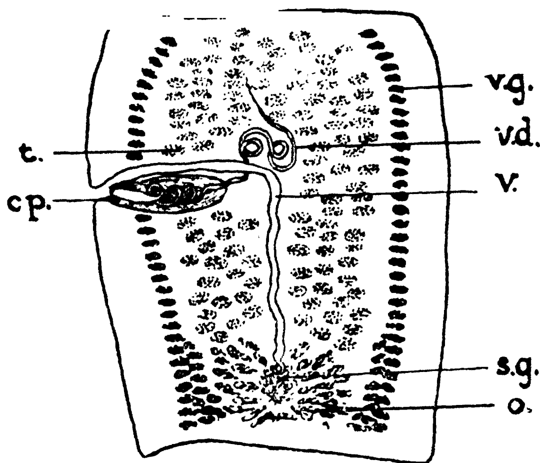


Fig. 192.—*Balanobothrium parvum.* Mature segment, × 112. (After Southwell.)

extremity of the ovary there are two or more rows. Each acinus is cylindrical, and lies with its long axis parallel to the transverse axis of the segment.

Shell Gland. This consists of a granular condensation distributed as a small globular mass round the fertilization canal.

Uterus. No gravid segments were seen. In the most mature ones the uterus consisted of a tube with lobulated walls running forwards in the antero-posterior axis of the segment ; eggs unknown.

The form of the head places the worm in the genus *Balanobothrium* Hornell, emended. It differs from *B. tenax* Hornell, the only other species within the genus, in being very much smaller and in having fewer testes.

Genus VI. POLYPOCEPHALUS Braun, 1878.

Synonyms:—*Parataenia* Linton, 1889.
Thysanobothrium Shipley & Hornell, 1906.
Anthemobothrium Shipley & Hornell, 1906.

Braun in 1878 erected the genus *Polypocephalus* with the following characters:—"Head subglobular with four suckers. Viewed *en face* it is square and flat; in the centre there is an opening leading into a sac-like cavity; glands seem to open into this cavity. Round its periphery there are sixteen unarmed tentacles. Genital pores ?"

Type-species:—*Polypocephalus radiatus* Braun, 1878.

Key to Species.

Tentacles feather-like	*P. pulcher*, p. 346.
Tentacles simple and tubular	*P. radiatus*, p. 342.

(1) **Polypocephalus radiatus** Braun, 1878. (Figs. 193, 194, & 195.)

Synonyms:—*Thysanobothrium uarnakense* Shipley & Hornell, 1906.
Parataenia elongatus Southwell, 1912.

From *Dasybatus uarnak* and *D. kuhli*, Pearl Banks, Ceylon. Hornell; Southwell. Also from *D. sephen*, Chilka Lake, Orissa, India. Southwell.

This worm, of which Braun had only two fragments, one with a head, measures about 2·5 cm. in length; the head is globular and bears four suckers, terminating anteriorly in a muscular ring, median to which there are sixteen hollow cylindrical tentacles radiating outwards. In the centre of the head there is a small os. The dimensions of the worm are as follows:—Length of head, 346 μ; breadth of head, 356 μ; length of tentacles, 339 to 396 μ; breadth of tentacles, 48 to 67 μ; diameter of os, 5 to 11 μ. Segmentation begins a little behind the head; the last segments are barrel-shaped and measure 452 to 549 μ in length and 339 μ in breadth. The worms were apparently immature, as the genital organs are not described.

Linton in 1889, apparently unaware of Braun's genus *Polypocephalus* (for he does not refer to it), created the genus *Parataenia*, with the following characters:—"Body tæniæform, articulate. Head subglobose, with four small opposite sessile bothria. Terminal os with sixteen protractile tentacular proboscides. Genital apertures marginal." He was of opinion that the genus was related to *Tænia* and that the "tentacular proboscides" were probably homologous with the rostellum of the avian Tæniidæ.

It appears undesirable to apply the term proboscides to the tentacular outgrowths, as they differ from the proboscides found in the order Trypanorhyncha. Linton's figure of the head shows that bothridia (lappet-like outgrowths) are absent; as the scolex bears four suckers, or acetabula, he placed it in the family Tæniidæ. He apparently made no distinction between bothria and acetabula, for he refers to the suckers in *Paratœnia medusia* as "bothria or acetabula." It is usual to apply the former term to grooves found along the sides of the head which possess no special musculature, as in *Dibothriocephalus latus*, and to restrict the latter to hemispherical cups which possess a special and strongly developed musculature.

The characters of the genus are as follows:—Strobila segmented. Head subglobular, with four acetabula. There is a terminal sucker from which arise a number of retractile tentacles.

Shipley and Hornell in 1906 created the genus *Thysanobothrium*, with the following characters:—"Length 7 cm.,

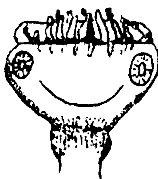


Fig. 193.—*Polypocephalus radiatus.* Head. × about 20. (After Shipley and Hornell.)

posterior proglottides being 1·5 mm. to 2 mm. long. Head squarish, with a sheath bearing four minute suckers at the angles; within the sheath a rounded knob, and between the sheath and the knob a ring of some twenty finger-like tentacles stretched forward. Neck long. Genital pores very irregularly alternate."

These characters agree exactly with those ascribed to the genus *Polypocephalus* by Braun in 1878, with the exception that Shipley and Hornell mention the presence of a terminal "knob" lying in front of the tentacles, although in the only species of this genus which they described this knob or myzorhynchus is not figured. They also state that the tentacles "are very curious, and, as far as we know, are unique amongst Cestoda." There can, I think, be no doubt that the genus *Thysanobothrium* Shipley and Hornell, 1906, is identical with *Polypocephalus* Braun, 1878.

Thysanobothrium uarnakense Shipley & Hornell, 1906.

The worm measures up to 7 cm. in length, the posterior proglottids being 1·5 to 2 mm. in length and 1 mm. in breadth. Anteriorly the worm is about 300 μ in breadth; the head has a diameter of at least 500 μ, and is squarish and yet subglobular, with four minute suckers. The latter are borne on a cup-like external bowl which surrounds a central portion, and between these two parts about sixteen to twenty simple tentacles protrude. The neck is about 5 mm. in length; the segments are not salient and the genital

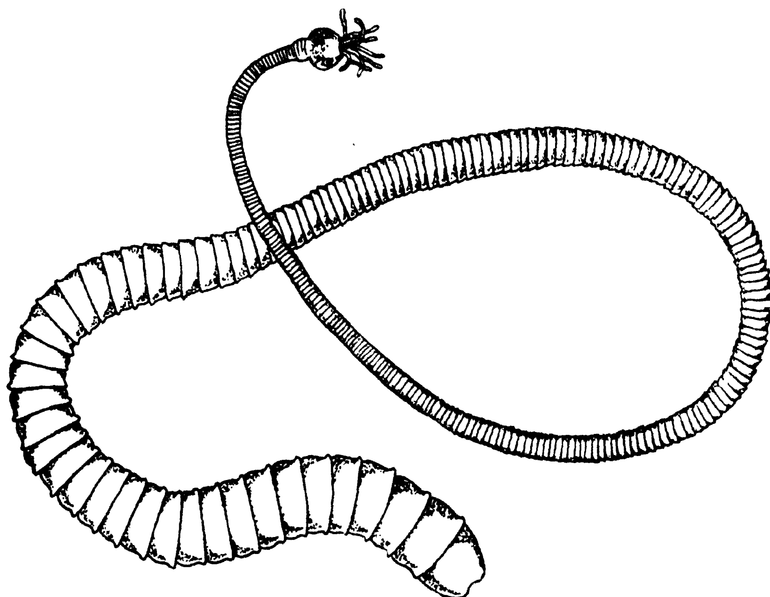


Fig. 194.—*Polypocephalus radiatus*. Entire worm, × 10. (After Southwell.)

pores are irregularly alternate. Details of the anatomy of the worm are not given. The species is inseparable from *P. radiatus* Braun, 1878.

Parataenia elongatus Southwell, 1912.

The worm attains a maximum length of 5 cm. and a breadth of 1 mm. It is oval in cross-section; all the segments are much broader than long and have salient posterior margins.

Head. The head measures from 380 to 500 μ in length and 420 μ in breadth; it bears four suckers, each of which has a diameter of about 80 μ. It is terminated anteriorly by a

large and deep fossa from which about sixteen digitate tentacles arise. These are retractile and are also capable of being elongated to two or three times the length of the head, the appearance of the latter being very different when the tentacles are extruded from what it is when they are retracted.

Neck. The neck is slightly narrower than the head and has a length of about 700 μ ; it gradually merges into the segments. Both the cortical and medullary parenchyma are notably spongy.

Excretory System. There are two vessels of about the same size running along each lateral margin ; they vary in diameter between wide limits in different segments of the worm.

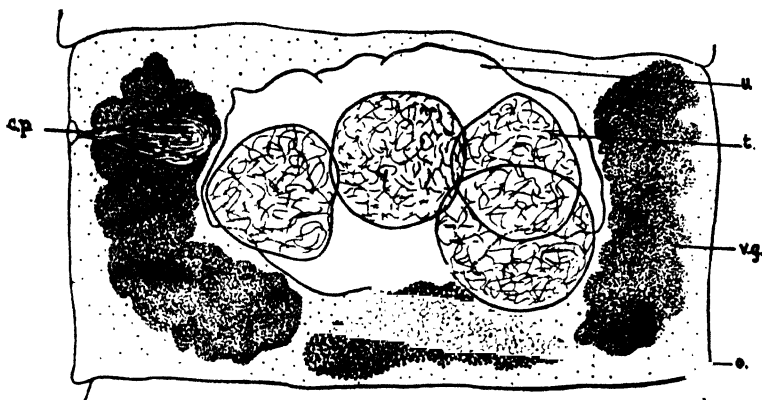


Fig. 195.—*Polypocephalus radiatus.* Mature segment, × 212. (After Southwell.)

Nervous System. There is a single nerve running along each lateral margin lying externally to the water vessels.

Muscular System. No circular fibres are to be seen in transverse sections in the region of the testes, so that they are either entirely absent or very scanty. The diagonal fibres are fairly prominent ; the longitudinal muscles are also well developed, and consist of a large number of small bundles four or five deep transversely, which decrease in size towards the periphery.

Testes. There are four testes, which are enormous in comparison with the size of the segment ; they almost completely fill the latter and each has a diameter of about 75 μ.

Vas deferens. The cirrus pouch is pyriform, but very small and inconspicuous ; it measures about 55 μ in length and 36 μ in breadth ; it appears to lie posteriorly to the vagina, but this

point was not definitely established. The cirrus bears a small number of spines near its extremity. Inside the pouch the vas deferens forms a small coil.

Ovary. This is a bilobed organ situated quite posteriorly; at its lateral extremities it expands fanwise. Under high magnifications it has a dense granular appearance.

Vagina. From the pore the vagina runs in front of the cirrus pouch in the transverse direction. It then turns backwards to the centre of the ovary, where it dilates into a small receptaculum seminis.

Shell Gland. This is a small granular organ having a diameter of about 23 μ and situated just posteriorly to the receptaculum seminis.

Vitelline Glands. These consist of a single row of very large glands, each one having a length of 30 μ; they lie with their long axes parallel to the transverse axis of the segment along each lateral margin. On the pore side there are five acini only, all of which lie posteriorly to the cirrus pouch, whilst aporally there are nine acini; they all appeared to be disintegrating.

Uterus. The uterus arises as a tube running in the median line forwards from the ovary. Its walls become lobulated, and eventually it fills the entire segment; uterine pore apparently absent.

Eggs. Unknown.

(2) **Polypocephalus pulcher** (Shipley & Hornell, 1906). (Fig. 196.)

Synonym:—*Anthemobothrium pulchrum* Shipley & Hornell, 1906.

From *Dasybatus sephen*, Pearl Banks, Ceylon. Hornell.

The characters of the genus *Anthemobothrium*, which contains one species only, are:—" 14 mm. long when preserved. Head about 1 mm. in diameter, almost spherical, with four small suckers in the hinder half, and fourteen feathered bothridia radiating over the anterior half. Neck narrow and short. Proglottides slightly overlapping their successors. The skin is faintly striped. The uterus in the posterior proglottides occupies almost all the space and is crowded with ova." (*Shipley & Hornell.*)

The only difference between the genera *Anthemobothrium* and *Polypocephalus* is that in the former the tentacles are said to be feather-like, whereas in *Polypocephalus* they are simple and tubular. The writer regards this difference as being of specific value only, and accordingly considers the genus *Anthemobothrium* synonymous with *Polypocephalus*, the latter having priority.

Anthemobothrium pulchrum was described by Shipley and Hornell as follows:—" A single example of this beautiful and remarkable Cestode was found amongst the crowd of

Tetrarhynchus leucomelanus and *Prosthecobothrium walga* [*sic* T. S.] taken from the intestine of a *Trygon sephen* captured in Dutch Bay.

"It measures 14 mm. in length when preserved in formaline, and as the posterior segments are crowded with eggs, it is apparently a full-grown worm. The head, which is almost spherical and as broad as it is long, measures just under 1 mm. across. The neck is very slender and short, and the body gradually, but slowly, broadens until the last segments are about 0·6 mm. broad by 0·9 mm. or 1 mm. long. The head consists of a basal hemisphere bearing four equidistant, small, rounded suckers. From the distal end of this basal part

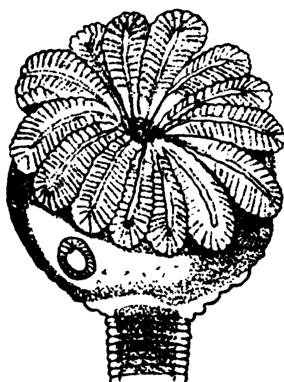


Fig. 196. - *Polypocephalus pulcher*. Head, × 40. (After Shipley and Hornell.)

emerge fourteen radiating bothridia, which are flattened down and look like so many neatly arranged ostrich feathers or frilled petals of a flower. The neck is narrow and short. The proglottides soon appear, at first much wider than long, but by the middle of the body they are square, and behind are twice as long as they are broad. The genital pore is not clearly visible, but some proglottides seemed to show an aperture on the flat surface near the anterior end. The uterus arises also at this end and is soon evident as a clear coiled tube. The divisions between neighbouring coils soon break down, and in the last proglottis the uterus, crammed with eggs, occupies almost all the space in the segment.

"Each segment has a very short lip posteriorly, which slightly overlaps the succeeding one. There is also a curious arrangement, probably of glands, in the skin, which gives the Cestode a longitudinally striped appearance, darker bands where the glands are present alternating with lighter areas where they are not."

Genus VII. CALYCOBOTHRIUM (Southwell, 1911).

Synonym :—*Cyclobothrium* Southwell, 1911.

Body segmented. Head shaped like a daisy with a central myzorhynchus bearing (?) four suckers, and surrounded externally and posteriorly by a frill of about fourteen hollow, unbranched, digitate, sucker-like tentacles arising from the base of the myzorhynchus. Genital pores marginal.

Type-species :—*Calycobothrium typicum* (Southwell, 1911).

The writer erected the genus *Cyclobothrium* to accommodate a single species (*C. typicum*) closely related to *Polypocephalus* Braun, 1878. As the name proved to be already occupied, it was changed to *Calycobothrium*. The genus differs from *Polypocephalus* in possessing a myzorhynchus which bears suckers, and which is situated in front of the tentacles, whereas in *Polypocephalus* there is no myzorhynchus, and the suckers are borne on the head, which is situated posterior to the tentacles.

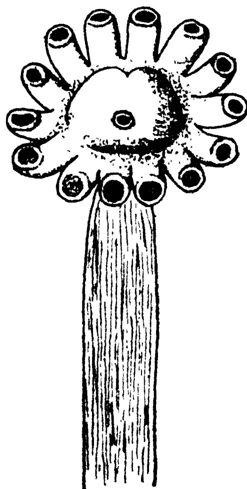


Fig. 197.—*Calycobothrium typicum*. Head, × 25. (After Southwell.)

Calycobothrium typicum (Southwell, 1911). (Figs. 197 & 198.)

Synonym :—*Cyclobothrium typicum* Southwell, 1911.

From *Stoasodon narinari*, Pearl Banks, Ceylon. Southwell.

The worm measures 8 cm. in length : the head is 500 μ in length and 1 mm. in breadth ; it consists of a large, central, slightly bifid myzorhynchus bearing (?) four small suckers.

From the base of the myzorhynchus about fourteen hollow, unbranched, digitate, sucker-like processes arise which spread out in a plane almost at right angles to the long axis of the worm. Neck 2 mm. in length; greatest breadth of the worm 1·7 mm. Posterior segments 2 mm. in length. Genital pores irregularly alternate; details relating to the muscular, excretory, and nervous systems are not known.

Testes There are about 125 testes, of which some twenty-four lie posteriorly to the cirrus pouch on the pore side. Each has a diameter of about 36 μ.

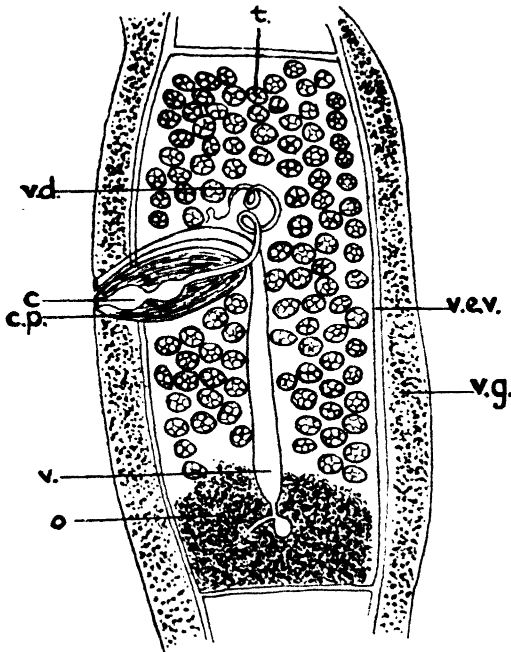


Fig. 198.—*Calycobothrium typicum.* Mature segment. × 112. (After Southwell.)

Vas deferens. The cirrus pouch extends halfway across the segment and measures about 150 by 75 μ. The cirrus is dilated and bears a few spines; a portion of the vas deferens usually lies coiled within the pouch; it is dilated at one point into a small internal seminal vesicle. Outside the pouch the vas deferens narrows considerably, and is thrown into a number of small and closely-set coils which lie anteriorly in the middle line, just in front of the bend in the vagina. The cirrus pouch lies posteriorly to the vagina, and the genital pores are

irregularly alternate, being situated a little in front of the middle of the lateral margin.

Ovary. The ovary consists of densely granular material, and it occupies the whole of the posterior quarter of the segment.

Vagina. From the pore the vagina runs in front of the cirrus pouch in the transverse direction; turning sharply backwards, it proceeds to the mid-ovarian region, gradually dilating posteriorly. It then narrows suddenly and again dilates into a rounded receptaculum seminis. The latter lies in the middle of the ovary and has a diameter of about 30 μ. The maximum diameter of the vagina is about 36 μ. No shell gland could be seen.

Vitelline Glands. These consist of two broad bands of acini, lying externally to the water vessels and extending the whole length of each segment except where interrupted by the vagina and cirrus pouch; each acinus has a diameter of about 4 μ.

Uterus. The uterus was not developed; eggs unknown.

There can be no doubt whatever that tentacles are characteristic of the genera *Polypocephalus* Braun, 1878, and *Calycobothrium* (Southwell, 1911).

Shipley states tnat in *Tetragonocephalum trygonis* Shipley & Hornell, 1905 (=*Tylocephalum trygonis* Shipley & Hornell, 1906), the suckers have a minute orifice, and "from these suckers small papillæ protrude, passing through the orifice."

Genus VIII. STAUROBOTHRIUM Shipley & Hornell, 1905.

Shipley and Hornell defined the above genus as follows:—"Cestode with large cruciform head, without hooks, genital pore lateral, no neck. From the intestine of *Ætiobatis narinari*, Ceylon Pearl Banks."

Type-species:—*Staurobothrium ætobatidis* Shipley & Hornell, 1905.

Staurobothrium ætobatidis (Shipley & Hornell, 1905). (Figs. 199, 200, & 201.)

From *Stoasodon narinari*, Pearl Banks, Ceylon. Hornell; Southwell.

"Head without hooks or any armature, it consists of four well-marked arms projecting from a centre, like the arms of a Maltese cross; each arm ends in a shallow sucker; anteriorly where the arms meet is a low annulated papilla representing the rostrum, but, as said above, there are no hooks. There is no neck. Each proglottis overhangs the one which succeeds it by salient angles forming a funnel-shaped skirt. The genital opening is on one side. The uterus, when full of ova, is

follicular. The average length of the worm, with about 100 proglottides, is 15 mm., the average width from 0·5 mm. to 0·7 mm." (*Shipley & Hornell.*)

Fig. 199.

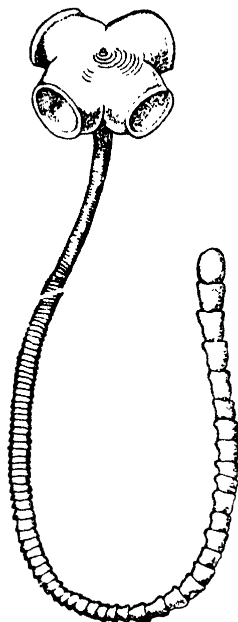
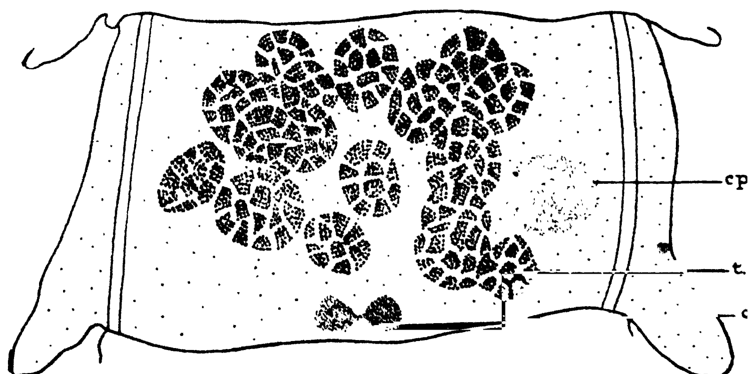


Fig. 200.



Staurobothrium ætobatidis.

Fig. 199.—Entire worm, × 6. (After Shipley and Hornell.)
Fig. 200.—Immature segment, showing testes and rudiments of the cirrus pouch and ovary, × 212. (After Southwell.)

Head. The head measures about 600 μ in length and from 900 μ to 1·5 mm. in breadth. It consists of four powerful suckers borne on very short pedicles and arranged like a Maltese cross. The suckers have a diameter of from 510 to 680 μ, and the pedicle measures about 75 μ when contracted.

The terminal papilla noted by Shipley and Hornell appears to be variable. The head is very muscular and, when mounted, its anterior face is seen to be traversed by strong muscles

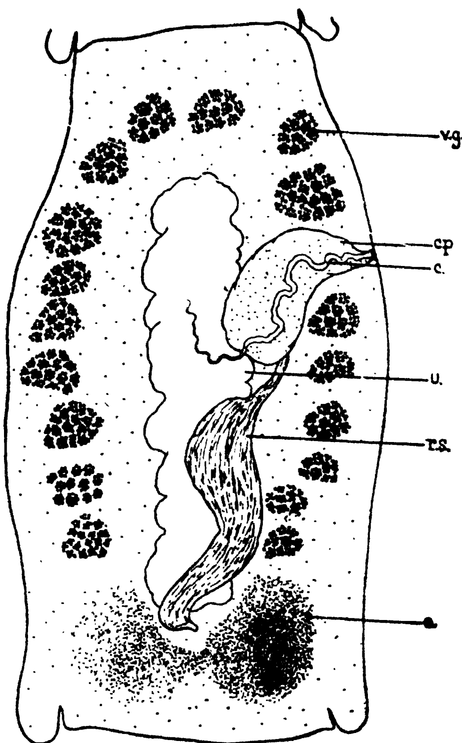


Fig. 201.—*Staurobothrium ætobatidis.* Mature segment, × 212. (After Southwell.)

arranged in a cross. The suckers are likewise very muscular. There is no neck.

The genital pores are irregularly alternate and are situated, in immature segments, either a little in front of or a little behind the middle of the lateral margin. In the mature proglottides they usually lie in front of the centre of the lateral margin.

Nothing is known about the muscular, excretory, and nervous systems.

Testes. These appear very early, and are almost fully developed before the cirrus pouch and ovary appear. There are about twenty-four testes; at first they occupy the centre of the segment, but as they mature they become scattered, and then they occur practically over the whole of the dorsal surface. Each testis has a diameter of about 50 μ.

Vas deferens. The cirrus pouch is pyriform and runs backwards and only slightly towards the middle, so that the whole sac appears to be nearly parallel to the lateral margin of the segment. When fully developed it measures about 120 μ in length by 55 μ in breadth; it lies posteriorly to the vagina. The cirrus forms a number of coils within the pouch and appears to be unarmed. Outside the latter the course of the vas deferens is very short; seminal vesicle absent (?).

Ovary. This is a bilobed organ situated posteriorly, and presenting a homogeneous granular appearance.

Vagina. The opening of the vagina lies in front of that of the vas deferens; from the pore the vagina curves and runs posteriorly, dilating into a very large muscular receptaculum seminis. Shell gland minute or absent.

Vitelline Glands. These are situated laterally and consist of a few very large acini which stain deeply, and, as a result, are very conspicuous in stained specimens. They only appear after the uterus has developed.

Uterus. The immature uterus consists of a tube with lobulated walls running along the antero-posterior axis of the segment. The form of the gravid uterus is unknown.

Genera of uncertain Systematic Position, but probably belonging to the Family Lecanicephalidæ.

Genus I. **ENIOCHOBOTHRIUM** Shipley & Hornell, 1906.

"Small Cestode, ranging from 6 mm. to 12 mm. in length. Head unarmed, with four suckers, rostellum conspicuous. Body divided into several regions, first a narrow neck of three or four segments; secondly, an oval region of eighteen segments, which get broader until about the tenth proglottis and then narrow again—the segments of this region overlap like a many-caped cloak; thirdly, a second very narrow region of eighteen segments, all about the same size; fourthly, the reproductively ripe region of six to eight segments rapidly maturing and becoming very large, the last, and in some cases the last two, being as large as the rest of the body. The reproductive pores are lateral and alternating; the cirrus bulb and cirrus are very large, and the latter has a broad band of chitinous spicules." (*Shipley & Hornell.*)

Type-species:—*Eniochobothrium gracile* Shipley & Hornell, 1906.

Eniochobothrium gracile Shipley & Hornell, 1906. (Fig. 202.)

From *Rhinoptera javanica*, Pearl Banks, Ceylon. Hornell.

The following is an abstract of the original description of this species:—In the living condition the worm measures 12 mm.; preserved specimens measure about 5 mm. The

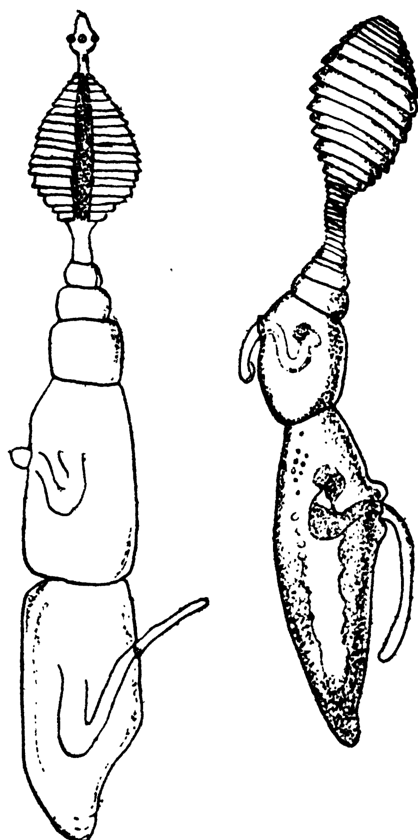


Fig. 202.—*Eniochobothrium gracile.* Entire worms, × 30. (After Shipley and Hornell.)

head bears four suckers and an unarmed rostellum. The neck is either very short or absent, and is followed by an expanded portion of the strobila consisting of about eighteen segments, the edges of which are salient. Behind this expansion the strobila suddenly becomes narrow, the narrow portion again containing about eighteen segments; but it is much shorter in length than the preceding portion of the strobila. Behind this second portion, there are six or eight segments

which rapidly increase in size, the last segment being as long as the rest of the worm. The cirrus sac is median and conspicuous, and a portion of the cirrus is armed. The genital openings are lateral and alternating; only traces of the vitellaria and testes were noted by the authors, and thus the anatomy of the worm is not known. . . . The peculiarities of this cestode are so marked that it deserves to be recognized as at least a new genus, if not representative of a new family. Until we know more of its anatomy, it is probably wiser to confine ourselves to the establishment of a new genus, and we suggest the name of *Eniochobothrium*, in view of the cestode's many-caped-coachman-like appearance.

This worm was described from two or three specimens, and its anatomy is entirely unknown. The presence of four suckers on the head allies it to the family Lecanicephalidæ; it is impossible to classify it further. It is not improbable that the peculiar appearance of the strobila may be an abnormal condition, but, even if such is the case, the head appears to be distinctive of a new genus.

Genus II. **DISCOBOTHRIUM** van Beneden, 1870.

Synonym :—*Hornellobothrium* Shipley & Hornell, 1906.

Van Beneden in 1870 figured the head of a worm, two examples of which he obtained from the intestine of *Raja clavata*, and which he named *Discobothrium fallax*. He gave no description of the worm, nor did he define the characters of the genus.

Braun (1900) described the head as having a large myzorhynchus and four small bothridia; he placed the worm in the order Tetraphyllidea, and in the family Phyllobothriidæ, as a subgenus of *Echeneibothrium*.

Monticelli (1890) and Olsson (1893) were of the opinion that *D. fallax* was identical with *Echeneibothrium variabile* van Ben.

Lönnberg (1889), however, considered that both the genus *Discobothrium* and the species *fallax* were distinct, and with this opinion Beauchamp (1905) agreed.

Hornellobothrium Shipley & Hornell, 1906.

"Very minute, 2 mm. in length. Head with rostellum and four suckers. No neck, but the body behind the head expands into a flattened region, sometimes like the head of a cobra; some twenty segments make this; the breadth then contracts and the proglottides become cylindrical, cuticle finely striated. Reproductive pores alternate, slightly irregular." (*Shipley & Hornell.*)

Type-species :—*Hornellobothrium cobraformis* Shipley & Hornell.

Discobothrium cobraforme (Shipley & Hornell, 1906). (Fig. 203.)

Synonym :—*Hornellobothrium cobraformis* Shipley & Hornell, 1906.

From *Stoasodon narinari*, Pearl Banks, Ceylon. Hornell.

"Great numbers of this curious and very minute species were found in the spiral intestine of *Ætiobatis narinari* ; five of these were sent to England. They are so small as not to be

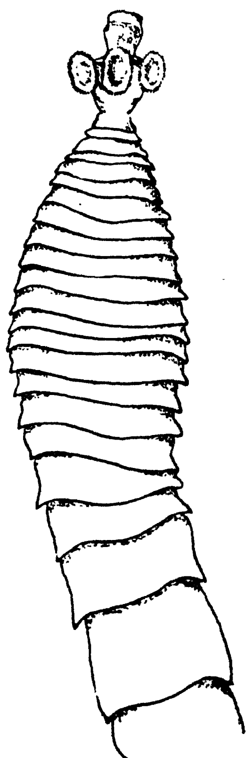


Fig. 203.—*Discobothrium cobraforme*. Anterior end, × 100. (After Shipley and Hornell.)

much more than visible to the naked eye, for although they are . . . 2 mm. in length, they are of an extreme tenuity in breadth, looking like little bits of very fine white silk.

"When alive, these Cestodes have a head with knob-like rostellum, on a constricted stalk ; this emerges from a broader squarish base, whose angles bear four deep suckers. The whole is capable of considerable expansion and contraction ; and constitutes the head. There is no neck, the proglottides

beginning immediately after the head. The first twenty proglottides widen out to form a broad flattened part of the body, in outline like the inflated hood of a cobra. These proglottides are all many times as broad as they are long, and the ratio of these diameters is greatest about the tenth or eleventh segment. About the twenty-first or twenty-second segment the proglottides become, perhaps, twice as broad as long and by the twenty-fourth they are square ; the remaining four or five proglottides are longer than broad, but the longest is never more than twice as long as broad. The posterior edges of the proglottides overhang the succeeding segments, but the extent to which this is done varies with the state of the contraction or expansion of the body. The cuticle is finely striated. The reproductive pores are alternate, but rather irregularly so, two consecutively left or right sometimes appearing." Habitat:—*Ætobatis narinari*, in the spiral intestine. (*Shipley & Hornell.*)

The figures of the head of *D. fallax* and *H. cobraforme* lead one to conclude that the genus *Hornellobothrium* is synonymous with *Discobothrium*; the species *H. cobraforme* (*D. cobraforme*) is, however, different from the species *D. fallax*.

Superfamily V. PROTEOCEPHALOIDEA, nov.

Synonym:—Proteocephalidæ La Rue, 1911.

Historical Account.

The confusion which exists with reference to the classification of the genera and species included in this superfamily is so great that it is not possible at present to do more than indicate the various ways in which systematic work on the group has been attempted during recent years.

The anatomy of a mature proteocephalid segment resembles that of a typical phyllobothrian in some detail, but gravid segments of the former differ from those of the latter in that the uterus usually consists of a wide, central, longitudinal stem which bears lateral pouches. Further, a uterine pore, or a number of pores, commonly occur on the ventral surface of the gravid segments (only), whereas in phyllobothrians uterine pores are usually absent. In addition, the head differs widely from that of a phyllobothrian. In the latter it consists of four ear-like lappets, whilst in the former it is a solid structure bearing four suckers (and in some cases with a terminal fifth sucker), thus resembling closely the head of a tænioidean. The range of morphological variations found

in species included in the superfamily is probably not greater than that found in most others, and the present chaotic condition is due to the fact that authors have utilized different characters in their definitions of genera.

Rudolphi in 1802 gave a brief description of two worms, one from the intestine of *Perca fluviatilis*, which he named *Tænia ocellata*, and another from the intestine of *Gasterosteus aculeatus*, which he named *Tænia filicollis*.

Blainville in 1828 used the name *Proteocephala* for a group of cestodes which contained *Caryophyllæus* Gmelin, 1790.

Weinland in 1858 erected the genus *Proteocephalus*, citing *T. ambigua* Dujardin, 1845, as the type. The name *Proteocephalus* was thus used by Weinland for a group of worms quite different from those to which Blainville had applied the name *Proteocephala*.

Lönnberg in 1894 erected the genus *Ichthyotænia* to contain the species described by Rudolphi.

Railliet (1899) stated that *T. ambigua* Dujardin, 1845, is synonymous with both *T. ocellata* Rudolphi, 1802, and *T. filicollis* Rudolphi, 1802.

Meggitt (1914 and 1927) maintains that as the name *Proteocephalus* Weinland, 1858, was preoccupied by *Proteocephala* Blainville, 1828, the name of the genus should be *Ichthyotænia*, and not *Proteocephalus*.

La Rue (1914) states that as Lönnberg named *Ichthyotænia filicollis* first in his list, that name is to be considered the type of the genus ; and that, unless Railliet's contention is wrong, *Ichthyotænia* Lönnberg, 1894, becomes a synonym of *Proteocephalus* Weinland, 1858. The latter point can never be determined, and the result is that some authors (Fuhrmann and Meggitt) retain the name *Ichthyotænia*, whilst others (La Rue and Woodland) retain *Proteocephalus* for the same group of worms.

Ariola (1899) placed the genus *Ichthyotænia* in a special family which he named Ichthyotæniidæ.

La Rue (1911) erected the family Proteocephalidæ, and included in it the genera *Proteocephalus* Weinland, 1858 ; *Corallobothrium* Fritsch, 1886 ; *Crepidobothrium* Monticelli, 1899 ; *Acanthotænia* Linstow, 1903 ; *Choanoscolex* La Rue, 1911 ; *Ophiotænia* La Rue, 1911.

In 1891 Monticelli erected the genus *Tetracotylus* for a worm obtained from *Silurus* sp. which resembled fairly closely others which had previously been referred to the genus *Ichthyotænia*. He named the species *Tetracotylus coryphicephala*. Monticelli did not designate a type-species, but Braun (1900) and Hall (1910) consider the above species to be the type of the genus. Braun concluded that the genus *Tetracotylus* was a synonym of *Ichthyotænia*.

As pointed out by La Rue (1911) and Meggitt (1914), the name *Tetracotyle* had previously been used by Filippi in 1855 for a group of immature trematodes. La Rue accordingly, in 1911, proposed the name *Monticellia* instead of *Tetracotylus*, and he pointed out that in the type-species, viz., *M. coryphicephala* (Monticelli, 1891), the testes, vitellaria, and uterus were situated in the cortex, and the worm therefore could not belong to his (La Rue's) family Proteocephalidæ, in which the genitalia were situated in the medulla. He therefore erected a new family, viz. Monticellidæ, for it.

In 1914 he ascribed the following characters, amongst others, to the genera noted below :—

Proteocephalus Weinland, 1858. No folds of tissue encircling base of head or enfolding suckers ; testes in a single field.

Corallobothrium Fritsch, 1886. Many irregular folds and lappets, which may enclose suckers as a corolla.

Crepidobothrium Monticelli, 1899. Posterior margin of sucker interrupted and re-entrant ; fifth sucker present. Testes in two lateral fields.

Acanthotænia Linstow, 1903. No fold of tissue on lappets. No rostellum, but a vestigial fifth sucker. Cuticle of head and part of body covered with minute spines.

Ophiotænia La Rue, 1911. Suckers without lappets ; no rostellum, but fifth vestigial sucker present. Testes in two lateral fields.

Choanoscolex La Rue, 1911. Folds of tissue partly covering suckers.

The following genera have since been placed in the two families Proteocephalidæ and Monticellidæ, viz. :—

(1) *Proteocephalus* Weinland, 1858=*Ichthyotænia* Lönnberg, 1894 ; (2) *Marsypocephalus* Wedl, 1861 ; (3) *Corallobothrium* Fritsch, 1886 ; (4) *Crepidobothrium* Monticelli, 1899 ; (5) *Acanthotænia* Linstow, 1903 ; (6) *Ophiotænia* La Rue, 1911 ; (7) *Choanoscolex* La Rue, 1911 ; (8) *Monticellia* La Rue, 1911 ; (9) *Ophidotænia* Beddard, 1913 ; (10) *Solenotænia* Beddard, 1913 ; (11) *Rudolphiella* Fuhrmann, 1916 ; (12) *Goezeella* Fuhrmann, 1916 ; (13) *Batrachotænia* Rudin, 1917 ; (14) *Gangesia* Woodland, 1924.

Fuhrmann and Baer (1925) accept and emend La Rue's family Monticellidæ, placing in it the following genera :—

(1) *Ephedrocephalus* Diesing, 1850=*Rudolphiella* Fuhrmann, 1916. Scolex globose, with folds of encircling tissue. Testes dorsal and lateral, situated in the cortical parenchyma. Uterus and part of the ovary situated in the medullary parenchyma ; vitellaria situated ventrally and in the cortical parenchyma. Type-species :—*Ephedrocephalus microcephalus* Diesing, 1850.

(2) *Monticellia* La Rue, 1911. Scolex globose, without folds of encircling tissue. Testes dorsal, situated in the cortical parenchyma. Vitellaria ventral and lateral, uterus ventral; both situated in the cortical parenchyma. Ovary partly in the cortical and partly in the medullary parenchyma. Type-species :—*Monticellia coryphicephala* (Monticelli, 1891).

(3) *Goezeella* Fuhrmann, 1916. Scolex globose, with folds of encircling tissue. Testes dorsal, situated in the cortical parenchyma. Vitellaria and uterus ventral, situated in the cortical parenchyma. Ovary almost entirely in the cortical parenchyma. Type species :—*Goezeella siluri* Fuhrmann, 1916.

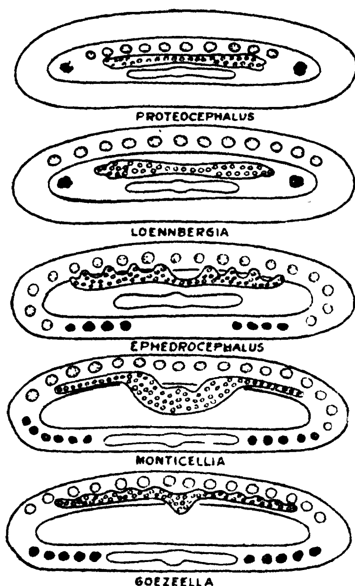


Fig. 204.—Diagrams of the internal anatomy of the genera of the Monticellidæ as compared with the genus *Proteocephalus*. The limits of the medullary and cortical parenchyma are indicated by a simple line. The testes are lightly dotted and the vitellaria heavily dotted. The ovary is represented with small circles and the uterus as an oblong sac. (After Fuhrmann and Baer, in P. Z. S.)

(4) *Lönnbergia* Fuhrmann & Baer, 1925. Scolex globose, without folds of encircling tissue. Testes in a single dorsal field, situated in the cortical parenchyma. Ovary, uterus, and vitellaria situated entirely in the medullary parenchyma. Type-species :—*Lönnbergia tanganyikæ* Fuhrmann & Baer, 1925.

These authors did not discuss the family Proteocephalidæ La Rue, 1911. Fig. 204 represents the positions occupied

by the genital organs in the above four genera and also in the genus *Proteocephalus* Weinland, 1858.

Woodland (1925, *a* & *b*) discusses at great length the characters on which the genera are based and the two families Monticellidæ and Proteocephalidæ established. He does not accept La Rue's family Monticellidæ, and of the numerous genera described he retains only four, thus :—

(1) *Proteocephalus* Weinland, 1858=*Ichthyotænia* Lönnberg, 1894. Synonyms :—*Crepidobothrium* Monticelli, 1889 ; *Acanthotænia* Linstow, 1903 ; *Choanoscolex* La Rue, 1911 ; *Ophiotænia* La Rue, 1911 : *Ophidotænia* Beddard, 1913 ; *Solenotænia* Beddard, 1913 ; *Corallobothrium* Fritsch, 1886 ; and apparently *Batrachotænia* Rudin, 1917.

(2) *Marsypocephalus* Wedl, 1861.

(3) *Monticellia* La Rue, 1911. Synonym :—*Goezeella* Fuhrmann, 1916.

(4) *Rudolphiella* Fuhrmann, 1916.

He defined these genera as follows :—

(1) *Proteocephalus* Weinland, 1858. With all the reproductive organs situated either in the medullary region of the parenchyma (where this is distinguishable from the cortex) or in the undivided parenchyma (when the internal longitudinal muscle sheath is absent). Vitellaria lateral, follicular, the follicles being closely grouped about a central conducting tubule. In fresh-water fishes, amphibians, and reptiles. Type-species :—*Proteocephalus filicollis* Rudolphi, 1802=*P. ambiguus* (Dujardin, 1845).

(2) *Marsypocephalus* Wedl, 1861. With testes situated in the dorsal cortex in a single field ; all other organs medullary. Vitellaria and all other organs as in *Proteocephalus*. In Siluridæ. Type-species :—*Marsypocephalus rectangulus* Wedl, 1861.

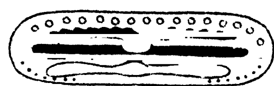
(3) *Monticellia* La Rue, 1911. With the " testes, vitellaria and uterus entirely outside the inner longitudinal muscle sheath. Vitellaria composed of scattered follicles which form broad lateral fields," mostly ventral in position. Testes lie in a single broad dorsal field between vitellaria. " Uterus ventral, with many lateral pouches." Ovary situated dorsally largely outside the longitudinal muscle sheath. Found in Siluridæ. Type-species :—*Monticellia coryphicephala* Monticelli, 1891.

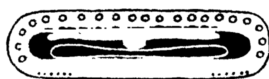
(4) *Rudolphiella* Fuhrmann, 1916. With the testes and vitellaria in the cortex, *i. e.*, outside the inner longitudinal muscle sheath. Vitellaria form broad lateral fields, ventrolateral in position. Testes lie in a single broad dorsal field between vitellaria. Uterus in the medulla and ventral in position, with many lateral pouches. Ovary situated dorsally,

with small projections from the lobes penetrating the upper part of the internal longitudinal muscle sheath. Found in Siluridæ. Type-species :—*Rudolphiella lobosa* (Riggenbach, 1896).

He emphasized the fact that those species of proteocephalid cestodes in which the testes are situated in the cortex fall into four groups, viz. :—

(1) *Proteocephalus* type, in which all the genital organs are situated in the medulla. (2) *Marsypocephalus* type, in which only the testes are in the cortex ; all the other genital organs being situated in the medulla. (3) *Monticellia* type, in which the testes, uterus, ovary, and vitelline glands are all in the cortex. (4) *Rudolphiella* type, in which the testes and vitelline glands only are in the cortex, the other genital organs being entirely or almost entirely situated in the medulla (fig. 205).





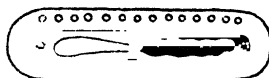




Fig. 205.—Diagrams illustrating the principal modes of disposition of the genital organs relative to the internal longitudinal muscle sheath in Proteocephalidæ. (After Woodland, in 'Parasitology.') The limits of the medullary and cortical parenchyma are indicated by a heavy line. The testes are represented by circles and the vitellaria by dots. The ovary is represented by heavy dots and the uterus as an oblong sac.

It will be seen that both Woodland (1925) and Fuhrmann and Baer (1925) agree with regard to the *Proteocephalus* type. *Lönnbergia* Fuhrmann & Baer, 1925, falls into Woodland's *Marsypocephalus* group ; Fuhrmann and Baer's *Ephedrocephalus* only differs from Woodland's *Rudolphiella* in that in the former the ovary invades slightly the cortical parenchyma. Both Woodland (1925) and Fuhrmann and Baer (1925) agree with regard to *Monticellia*; whilst Fuhrmann and Baer's

Goezeella only differs from their *Monticellia* in that the invasion of the ovary into the cortex is more complete. The distinction between Fuhrmann's *Goezeella* and La Rue's *Monticellia* is not and cannot be defined; consequently *Goezeella* must be regarded as identical with *Monticellia*.

The following table summarizes the points of difference between the genera :—

	Proteocephalus.	*Lönnbergia.*	*Ephedrocephalus.*	*Monticellia.*	*Goezeella.*
Testes ..	In medulla.	In cortex. Dorsal.	In cortex. Dorsal and lateral.	In cortex. Dorsal.	In cortex. Dorsal.
Ovary .	In medulla.	In medulla.	Partly in cortex, partly in medulla. Dorsal.	Partly in cortex, partly in medulla. Dorsal.	Almost wholly in cortex. Dorsal.
Vitelline glands.	In medulla.	In medulla. Lateral.	In cortex. Ventral.	In cortex. Ventral.	In cortex. Ventral.
Uterus ...	In medulla.	In medulla.	In medulla.	In cortex. Ventral.	In cortex. Ventral.

Woodland recognized two main groups of species within the genus *Proteocephalus* as defined by him, viz. :—(1) those of fresh-water teleostean fishes comprising forms with a small head, total absence of hooks and spines, testes in one continuous field, and in which the vagina always opens anterior to the cirrus. For this subgenus Woodland suggested the name *Teleostotænia*, since *Ichthyotænia* is, in his opinion, inadmissible. (2) Those typically found in ophidia and in a less degree in siluroids, amphibians, and chelonians, comprising those forms in which the scolex is large or small; rostellum present or absent; apical organ present or absent; spines usually absent; testes usually to some extent, or entirely, in two lateral fields; and with the vagina and cirrus apertures irregularly alternating as to which is anterior. For this large group or subgenus he suggested the name *Crepidobothrium*.

Seven genera have been erected on characters of the scolex, viz., the six described by La Rue (1924, *vide supra*) and *Gangesia* Woodland, 1925. These scolex characters include the presence or absence of spines, folds, and notched suckers. It is true that in some of these genera other morphological characters have also been utilized, such, for instance, as the fact that in some genera the testes are in two lateral fields, whilst in other genera they are in a single field.

Woodland (1925) concluded that "scolex characters cannot be utilized for the definition of genera either by themselves or in conjunction with other characters, since in very many cases species which are most unlike as regards their strobila possess similar scoleces, and *vice versa*, many forms similar

to each other in proglottid anatomy possess widely different scoleces." He also drew attention to the fact that within the genus *Acanthotænia*, in which the scolex is armed, the testes in some species are in two lateral fields, whilst in others they are in a single field. These two types are united into one genus owing to the fact that the head and the anterior part of the strobila are covered with minute spines.

It remains to be seen whether this scheme will prove satisfactory or not. The determination of the genera will necessitate sectioning both mature and gravid segments, and the latter are not always available. It is most probable that numerous cases will arise in which there is no division into medullary and cortical parenchyma or it is ill defined, and even where such a distinction does exist, portions of the genitalia on which a determination depends may lie partly in one and partly in the other, as, in fact, they do in Fuhrmann and Baer's two genera *Ephedrocephalus* and *Monticellia*. Further, in gravid segments the muscular system generally atrophies, in which event it may not be possible to determine the position occupied by the uterus and, perhaps, the vitelline gland. This scheme of classification, whilst appearing simple and satisfactory, may therefore become as impracticable in application as that which it aims at superseding.

Meggitt (1927) called attention to the "confusion at present existing in the families Monticellidæ La Rue, 1911, and Ichthyotæniidæ Ariola, 1899." He did not accept La Rue's family name Proteocephalidæ, on the ground that as the genus, *Ichthyotænia* Lönnberg, 1894, has precedence over *Proteocephalus* Weinland, 1858, so the family Ichthyotæniidæ Ariola, 1899, has precedence over Proteocephalidæ La Rue, 1911. After discussing at great length the morphological characters of the various genera in these two families, he asserts that the conclusions drawn by Woodland with regard to the varying position of the essential genital organs are too sweeping, and also that the characters of the scolex in these various genera, disregarded by Woodland, are of considerable importance. He adopts Fuhrmann and Baer's classification of the family Monticellidæ, but includes in it the genus *Marsypocephalus* Wedl, 1861.

He notes that the following genera have been placed in the family Ichthyotæniidæ Ariola, 1899.

(1) *Corallobothrium* Fritsch, 1866; (2) *Crepidobothrium*, Monticelli, 1889. (Synonyms:—*Ophiotænia* La Rue, 1911; *Ophidotænia*, Beddard, 1913; *Solenotænia* Beddard, 1913.) (3) *Ichthyotænia* Lönnberg, 1894; (4) *Acanthotænia* Linstow, 1903; (5) *Choanoscolex* La Rue, 1911; (6) *Batrachotænia* Rudin, 1917; (7) *Gangesia* Woodland, 1925.

He classifies the family as follows :—

Ichthyotæniidæ Ariola, 1899.

Tetraphyllidea.—Scolex simple or with posterior lobed collar, with four entire sessile suckers; if armed, only with small cuticular spines. A terminal organ present or absent. Genital pores marginal, alternating. Vitellaria lateral, follicular. Ovary bilobed, posterior. Uterus with median stem and broad, closely-packed lateral outgrowths. Adults in fish, amphibians, reptiles, and mammals. Larval stages, plerocercoid, with or without terminal invagination; in Entomostraca and (?) Turbellaria. Type-genus :—*Ichthyotænia* Lönnberg, 1894.

Genus (1) *Ichthyotænia* Lönnberg, 1894. (Synonyms :—*Acanthotænia* Linstow, 1903; *Batrachotænia* Rudin, 1917; *Choanoscolex* La Rue, 1911.) Scolex with or without apical organ of various shapes, but never with a rostellum armed with hooks. Testes in a single field. Vagina usually anterior to cirrus sac, occasionally posterior, never alternating, usually with a weak sphincter. Adults in fish. Type-species :—*Ichthyotænia percæ* (Mueller, 1780).

Genus (2) *Corallobothrium* Fritsch, 1886. Scolex with lobed and folded collar posterior to and partially obscuring the four suckers. External segmentation distinct. Genital ducts pass between longitudinal excretory vessels and ventral to the nerve. Testes in medullary parenchyma, numerous, in a single dorsal layer, but laterally to the uterus in several layers, filling the whole medulla. Ovary in medullary parenchyma, dorsal, slightly lobed. Adults in fish. Type-species :—*Corallobothrium solidum* Fritsch, 1886.

Genus (3) *Crepidobothrium* Monticelli, 1900. Scolex with or without apical organ of various shapes, never with a rostellum armed with hooks. Surface of scolex and suckers sometimes covered with fine spines. Testes in two lateral fields, with an occasional tendency to coalesce anteriorly. Vagina anterior or posterior to cirrus sac, usually with a well-developed sphincter. Type-species :—*Crepidobothrium gerrardi* Baird, 1860.

It will thus be evident that the classification of the species included in Woodland's conception of the family Proteocephalidæ is a matter of great difficulty, and one on which no two authors agree. The writer accepts Woodland's classification except so far as the genus *Proteocephalus* is concerned; but the genus *Gangesia* is retained. The former contains the greater bulk of the species, and is consequently large and unwieldy. There appears to be no reason why any stable character (if such exists) should not be used for dividing the genus merely as a matter of convenience. Such characters

are very limited in number, especially in view of the fact that the genitalia are confined to the medullary parenchyma. The features which have been considered in this connection are the following, and it will be noted how variable they are:—

(1) Whether the testes are in a double or a single field. Species are known in which it is difficult to determine whether the testes are in a single or a double field, as, for instance, in segments where, posteriorly, they are in two fields, whilst in the anterior part of it they extend right across it. It will thus be evident that, whilst the extreme or definite cases are easily recognizable, the intermediate types would be difficult to classify unless a third and separate genus was erected for their accommodation. But in any case it is abundantly clear that the types merge into each other by almost imperceptible gradations which defy the ingenuity of man to classify. For these reasons the writer is of opinion that the distribution of the testes is of specific value only, and offers no satisfactory grounds on which to erect genera.

(2) Meggitt notes that "the course of the genital ducts with reference to the longitudinal excretory canals appears to have been entirely ignored by authors. . . It is possible that this character when stated for every species may assist the separation of genera."

(3) There appears to be no valid reason against using characters of the head for the distinction of genera. Such features are used not only for the classification of the four main orders of cestodes, but also for the identification of genera such as, for instance, *Davainea*, *Dipylidium*, *Tænia*, etc.; and also it can be said that the only character common to the various species included in the family Anoplocephalidæ is the fact that the head is unarmed. In *Crepidobothrium* Monticelli, 1899, the posterior margins of the suckers are interrupted and re-entrant into the sucker cavity. The isolation into one genus of species showing such a character is not more artificial than the separation of those species into one genus which possess a rostellum armed with rose-thorn-shaped hooks. Again, in Woodland's genus *Gangesia* a very definite rostellum is present bearing hooks, and this fact is sufficiently striking, in the opinion of the writer, to warrant the retention of the genus.

(4) In the genus *Corallobothrium* folds of tissue occur which partly cover the suckers. Unfortunately, as pointed out by Woodland, the genera *Goezeella* Fuhrmann, 1916, and *Rudolphiella* Fuhrmann, 1916, have similar folds on the head; but anatomically the three genera differ among themselves profoundly in that in the two latter portions of the genital organs lie in the cortical parenchyma, whilst in the former the entire genital organs are situated in the medulla. If these forms are classified on characters of the head,

then they are all alike, and the name of the genus should be *Corallobothrium* Fritsch, 1886. If, however, we classify them on anatomical details, then the three genera are entirely distinct. It will thus be clear that the presence of lappets, etc., on the head cannot here be used alone as a generic character.

(5) The genus *Acanthotænia* Linstow, 1903, is characterized, amongst other things, by the fact that the cuticle of the scolex and anterior part of the body is covered with minute spines. It would appear that such a feature is sufficiently distinctive to warrant the retention of Linstow's genus *Acanthotænia*, but it has been found that other worms differing widely from species of *Acanthotænia* also have scoleces armed with minute spines. Thus in the two species of *Gangesia* described by Woodland the head not only bears an armed rostellum, but is also covered with spines. The presence or absence of spines on the head cannot therefore be regarded as of more than specific value.

It is admitted at once that the above distinctions are purely artificial. but all systems of classification, on whatever characters they are based, are the same, the difference being merely one of degree.

Magath (1929) is of opinion that " it does not seem wise at this time to accept Woodland's (1925) sweeping revision of the Proteocephalids, although there is argument in favour of it." The writer, however, adopts Woodland's classification, except that the genus *Gangesia* is retained on the ground that the presence of an armed rostellum is a character sufficiently striking and pronounced adequately to characterize and diagnose the genus.

The superfamily Proteocephaloidea is characterized as follows :—

Head unarmed or armed with minute spines and with four sessile suckers devoid of areolæ or accessory suckers. An apical organ is frequently present, and occasionally a distinct muscular rostellum. Vitellaria lateral, follicular, the follicles usually being closely grouped about a central duct when in the medulla, but when situated in the cortex spread out over a relatively broad lateral area. Ovary bilobed and posterior. Uterus with lateral diverticula and one or more median ventral uterine openings. Vitellaria, testes, ovary, and uterus usually within the inner longitudinal muscle sheath, but in certain genera one or more of these organs may be situated in the cortex. Habitat :—Intestines of fresh-water fish, amphibians, and reptiles.

Family PROTEOCEPHALIDÆ La Rue, 1911.

With the characters of the Superfamily.
Type-genus :—*Proteocephalus* Weinland, 1858.

Key to Genera.

Head without a rostellum .... PROTEOCEPHALUS, p. 368.
Head with an armed rostellum.......... GANGESIA, p. 382.

Genus I. PROTEOCEPHALUS Weinland, 1858.

Synonymy extensive, as indicated above.

Scolex without rostellum ; all reproductive organs situated either in the medullary region of the parenchyma (where this is distinguishable from the cortex) or in the undivided parenchyma (when the internal longitudinal muscle sheath is absent). Vitellaria lateral, follicular, the follicles being closely grouped about a ventral conducting tubule. In fresh-water fish, amphibians, and reptiles.

Type-species :—*Proteocephalus filicollis* (Rudolphi, 1802)= *Proteocephalus ambiguus* (Dujardin, 1845) Weinland, 1858.

In the present state of our knowledge it is not possible to give a key to the Indian species of this genus.

(1) **Proteocephalus shipleyi** (Linstow, 1903). (Fig. 206.)

Synonym :—*Acanthotænia shipleyi* Linstow, 1903.

From *Varanus* (*Hydrosaurus*) *salvator*, Horana, Ceylon ? Willey.

The worm was described from a single specimen which measured about 1·38 in length and 40 μ in breadth. Segmen-

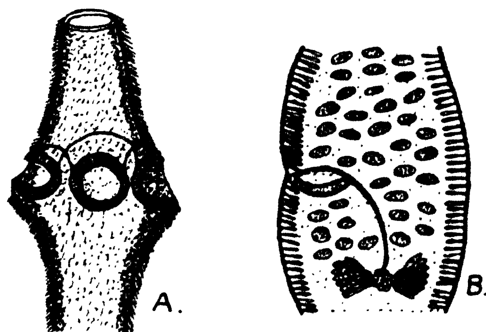


Fig. 206. *Proteocephalus shipleyi*. A, head, showing spinules ; B, mature segment, magnification unknown. (After Shipley.)

tation of the strobila was not evident anteriorly, and only indicated posteriorly by the position of the genital organs. All the segments were broader than long : the genital pores

were irregularly alternate and situated in the centre of the lateral margin of the proglottis. The scolex measured 240 μ in length and 180 μ in breadth; the rostellum was 120 μ in length, 100 μ in breadth, and unarmed; the cuticle of the scolex and of the body for a distance of 160 μ was beset with thickly-set fine bristles. There are about 50 testes in each segment. The cirrus sac is curved with the convexity anterior, and the organ opens behind the vagina. The ovary is bilobed and the vitelline gland is round. The eggs are not known.

(2) **Proteocephalus punicus** (Cholodkovsky, 1908) Hall, 1910. (Figs. 207, 208, & 209.)

Synonyms:—*Tænia punica* Cholodkovsky, 1908.
Ophiotænia punica (Cholodkovsky, 1908) La Rue, 1911.
Crepidobothrium punicum (Cholodkovsky, 1908) La Rue, 1911.

From the Malayan palm-civet (*Paradoxurus hermaphroditus*), Zoological Gardens, Calcutta. Southwell.

Probably the true host of this species is a snake. Cholodkovski obtained the type-species from a dog. Southwell and Adler (1923) recorded the worm from *Causus rhombeatus*, Freetown, Sierra Leone. this being the first record of the parasite from a snake.

The worm attains a length of 30 cm. and a breadth of 4 mm. It is composed of a large number of proglottides, the superficial segmentation not being distinct. The posterior ones are

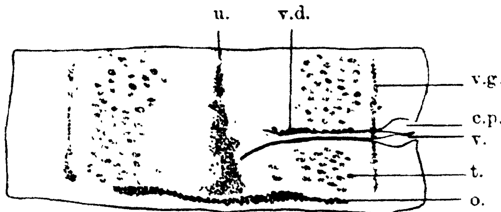


Fig. 207.—*Proteocephalus punicus*. Mature segment. × 35. (After Southwell and Adler.)

longer than broad; the genital pores are irregularly alternate and are situated near the middle of the lateral margin of the segment. The head is almost square and has a diameter of about 1·5 mm. The suckers have a breadth of about 700 μ.

The musculature consists of a series of (1) small subcuticular fibres, situated immediately beneath the cuticle; (2) a double layer of longitudinal muscles which are not strongly developed; (3) a few diagonal fibres; and (4) circular muscles which are very scanty.

There are two water vessels on each side, the ventral being

much larger than the dorsal. A single nerve runs laterally to the water vessels. The parenchyma is strongly developed.

The testes are confined to the lateral fields in front of the ovary and median to the vitellaria. There are from 170 to 230 in each segment: they are oval in shape, their long axes being horizontal. The cirrus pouch first becomes evident about 15 mm. behind the head; it lies anteriorly or posteriorly to the vagina and extends beyond the vitellaria, being up to

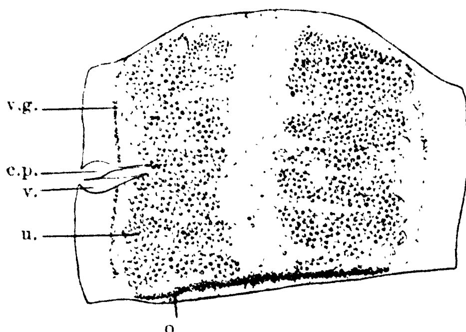


Fig. 208.—*Proteocephalus punicus.* Gravid segment, × 35. (After Southwell and Adler.)

670 μ in length. The cirrus is spiny and is continuous with an internal seminal vesicle, which latter occupies about two-thirds of the cirrus sac. The vas deferens lying outside the sac is coiled.

The ovary is long and narrow and is not bilobed: it is situated posteriorly. The vagina lies either anteriorly or posteriorly to the cirrus sac: it runs almost straight towards

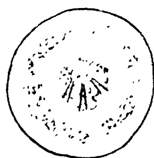


Fig. 209.—*Proteocephalus punica.* Egg, × 733. (After Southwell and Adler.)

the middle of the segment and then turns posteriorly. The vitellaria are lateral, and consist of small acini each measuring about 30 to 36 μ in diameter. The uterus is a straight tube running antero-posteriorly; in mature segments it has from eight to twelve lateral pouches on each side. There is a small shell gland situated immediately behind the middle of the

ovary. In transverse sections of segments in which the uterus was gravid no uterine pores were seen. The eggs are 30 μ in diameter, and in appearance resemble those of *Hymenolepis nana*. The oncosphere is from 13 to 15 μ in diameter. The embryophore has a thickness of about 3 μ.

(3) **Proteocephalus naiæ** (Beddard, 1913). (Fig. 210.)

Synonym:—*Ophidotænia naiæ* Beddard, 1913.

From *Naia tripudians*, United Provinces, India. Woodland, 1925.

The worms measure up to 10 cm. in length and have a maximum breadth of about 2·5 mm. The posterior segments are longer than broad. The genital pores are irregularly

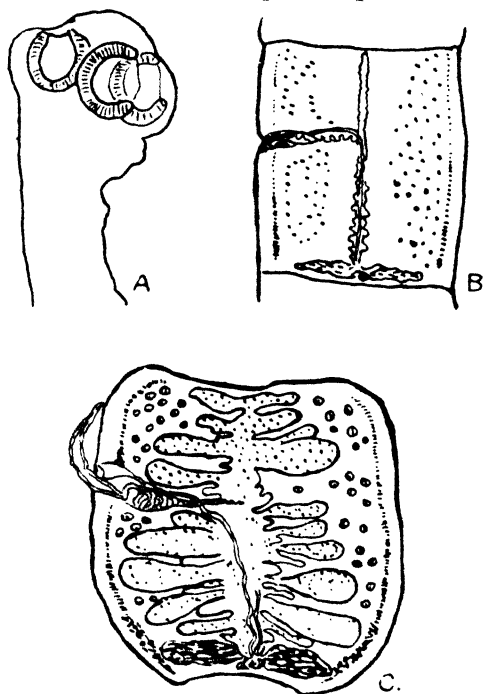


Fig. 210. *Proteocephalus naiæ*. A, head, ×87·5; B, mature segment, ×12; C, gravid segment, ×12. (After Woodland.)

alternate and are situated at the middle, or a little anteriorly to the middle, of the lateral margin of the segment. The neck measures from 3·5 to 6 mm. in length. The scolex is from 153 to 210 μ in length by 248 to 303 μ in breadth; there is no rostellum (apical organ) and cuticular spines are absent. The suckers are protrusile and are borne on the lobe of the scolex.

Male Genitalia. There are about 120 testes, situated in two quite lateral fields. The cirrus sac extends across about a quarter of the breadth of the segment and measures, when fully developed, from 498 to 531 μ in length by 83 to 107 μ in breadth, but it varies in size within wide limits; the cirrus is unarmed. The sac is sometimes posterior and sometimes anterior to the vagina.

Female Genitalia. The ovary is posterior, consisting of two lobes connected by an isthmus; the vagina is slightly dilated near its opening. The vitelline glands are arranged in a narrow antero-posterior strand along each margin of the segment. The shell gland lies posteriorly to the ovarian isthmus. The uterus consists of a median stem with from 16 to 25 lateral diverticula on each side. The median sac of the uterus opens by a number of pores on the ventral surface of the strobila. The egg measures about 26 μ and the contained embryo 9 to 11 μ.

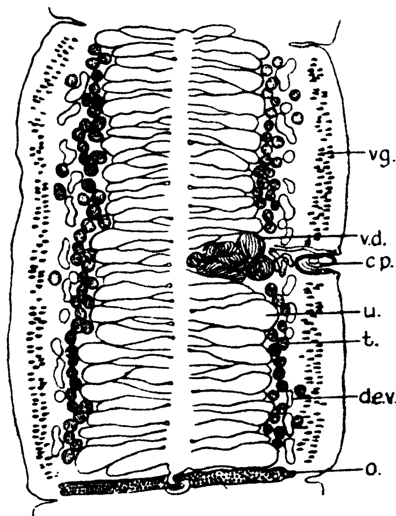


Fig. 211.—*Proteocephalus mönnigi.* Horizontal section of mature segment. magnification unknown. (After Fuhrmann and Baer.)

(4) **Proteocephalus mönnigi** (*Fuhrmann*, 1924). (Fig. 211.)

Synonym:—*Ophiotænia mönnigi* Fuhrmann, 1924.

From an unidentified snake, Burma. Meggitt.

The worm attains a length of about 5 cm. and a maximum breadth of 1·8 mm. As in other species of this genus, the segmentation of the strobila is indistinct. Gravid segments measure about 2·5 mm. in length and about 1·6 mm. in breadth. The genital pores are irregularly alternate and situated near

the middle of the lateral margin ; each pore opens into a rather deep genital atrium.

Muscular System. Transverse and dorso-ventral fibres are extremely scarce, the muscular system consisting principally of longitudinal fibres disposed in a more or less circular layer.

Excretory System. There is a dorsal and ventral vessel running along each lateral margin of the worm, the ventral being much larger than the dorsal and lying directly underneath it.

Nervous System. On each lateral margin of the worm there are three nerves, viz., a main nerve and two small accessory nerves, one dorsal and the other ventral to the large nerve.

Male Genitalia. There are from 50 to 70 testes, disposed in two clearly separated lateral fields. The vas deferens is very coiled and at places greatly dilated, probably functioning as a vesicula seminalis. The cirrus sac is small, measuring only 200 by 100 μ. An internal vesicula seminalis is absent, but the vas deferens within the sac is sometimes distended. The cirrus is large and muscular.

Female Genitalia. The ovary consists of a narrow transverse band situated extremely close to the posterior margin of the segment and passing laterally to the excretory vessels. The vagina lies anteriorly to the cirrus sac, and a small sphincter muscle is present. A receptaculum seminis is absent. The vitelline glands are in two lateral bands lying just internally to the longitudinal nerves. The uterus consists of a median stem with from 50 to 57 diverticula on each side, each one of which, however, is not single but double, and sometimes treble. Uterine pores are absent. The egg measures 30 μ in diameter and the embryo 13 μ.

(5) **Proteocephalus nilotica** (Beddard, 1913). (Fig. 212.)

Synonyms :—*Ichthyotænia nilotica* Beddard, 1913.
Ichthyotænia nilotica Southwell, 1916.
Acanthotænia biroi Southwell, 1922.
Proteocephalus beddardi Woodland, 1925.

From *Varanus bengalensis*, Orissa, India. Southwell. United Provinces, India. Woodland.

The worm varies in length from 4 to 8 cm. and has a breadth of 800 μ. The posterior segments may be nine times longer than broad. The genital apertures are irregularly alternate and are situated about the middle of the lateral margin of the segment. The scolex measures about 212 μ in length and 259 μ in breadth ; it is covered with cuticular spines which extend over the neck, and consist of a rostellum and a four-lobed base, each lobe carrying a sucker.

Male Genitalia. There are from 60 to 80 testes, which in some segments are in two fields, whilst in others they are in a single

uniform field. The cirrus sac is about a quarter the breadth of the segment, but when the worm is extended it may reach halfway across. It measures about 128 μ in length by 51 μ in breadth. The cirrus is armed with spines. The cirrus sac lies dorsally and apparently in front of the vagina.

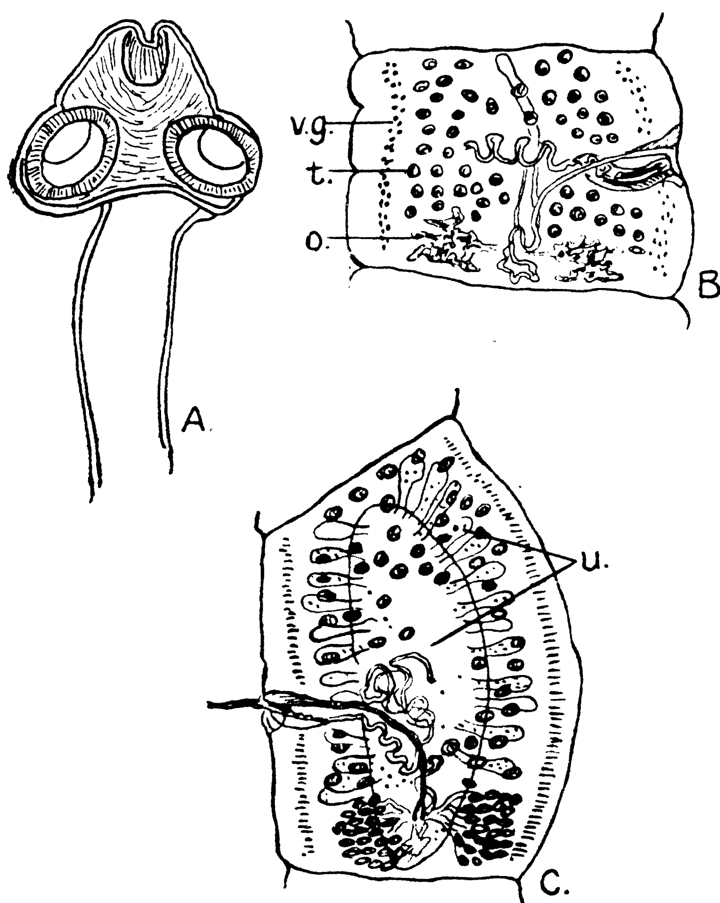


Fig. 212. —*Proteocephalus nilotica.* A, head, ×116; B, mature segment, ×52; C, gravid segment, ×23. (After Woodland.)

Female Genitalia. The ovary is posterior and bilobed, each half being composed of elongated follicles. As usual, the vitellaria consist of an antero-posterior strand along each lateral margin. Near the pore the vagina is enlarged to the size of the cirrus sac; it sometimes shows a dilatation mid-way between its opening and the ovary. The uterus is a

central stem with apparently from 15 to 20 lateral diverticula on each side; uterine eggs measure about 14 by 19 μ.

Southwell in 1916 recorded the occurrence of *Ichthyotænia nilotica* Beddard, 1913, from *Varanus bengalensis*, and there can be no doubt that Woodland's *P. beddardi* is the same worm.

The points on which Woodland erected his species are of such a minor character that it is difficult to believe that the two so-called species are different, in spite of the fact that one was obtained from an African and the other from an Indian monitor. There are numerous instances of species having a wide zoo-geographical distribution.

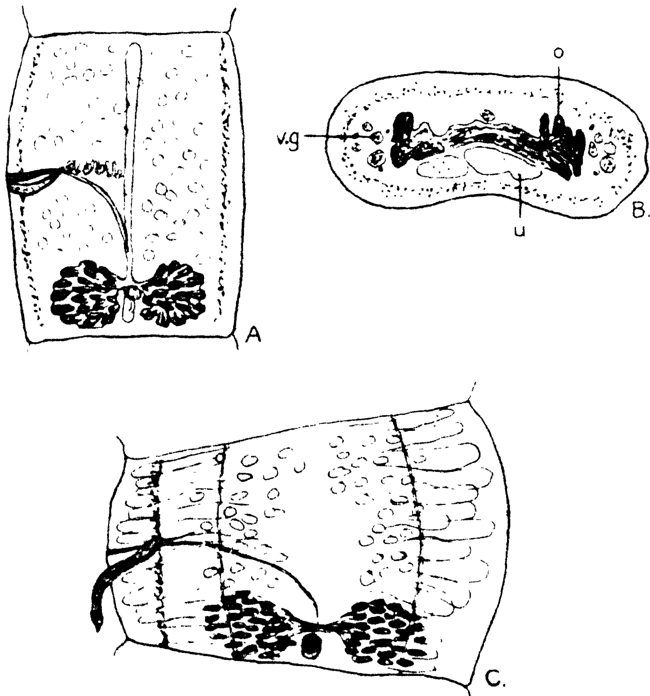


Fig. 213. *Proteocephalus tigrinus.* A, mature segment, × 35; B, transverse section of mature segment, × 50; C, gravid segment, × 24. (After Woodland, in 'Parasitology.')

(6) **Proteocephalus tigrinus** Woodland, 1925. (Fig. 213.)

From *Rana tigrina*, United Provinces, India. Woodland.

The worm measures from 3 to 4 cm. in length, with a maximum breadth of about 1·39 mm. The more posterior segments are longer than broad; the genital pores are irregularly

alternate, and are situated at the middle of the lateral margin of the proglottid. The scolex measures about 146 μ in length by 233 μ in breadth; it does not bear spines. There is a terminal apical sucker. The neck measures about 2 mm. in length.

The muscular system is poorly developed, and an inner longitudinal layer is entirely absent: the medulla and cortical parenchyma are thus indistinguishable. There are a few dorso-ventral fibres and a distinct subcuticular layer of longitudinal muscles.

Male Genitalia. There are from 70 to 110 testes situated anteriorly to the ovary, dorsally to the uterus, and in a single field. The cirrus sac is usually posterior to the vagina, but sometimes the reverse is the case: it measures about 200 μ in length by 50 μ in breadth, and extends over about one-fifth the breadth of the segment. The cirrus is unarmed.

Female Genitalia. The ovary is posterior and bilobed; the vagina, oviduct, and shell gland all lie dorsally to the ovarian isthmus. The vagina is dilated in the vicinity of the cirrus sac and a sphincter muscle is present. The vitelline gland consists of a lateral antero-posterior strip on each side. The uterus is a wide central stem, its posterior part being ventral to the ovary, with from 15 to 20 diverticula on each side extending to the vitellaria. The size of the egg is not known, but the embryo measures 11 μ

(7) **Proteocephalus ritæ** Verma, 1926. (Fig. 214.)

Synonym:—*Proteocephalus ritaii*, Verma, 1926.

From *Rita rita*, rivers of Northern India. Verma.

The worm attains a length of from 75 to 125 cm. and a maximum breadth of about 3 mm. It is composed of from 600 to 1000 segments. The posterior ones are longer than broad; the genital pores are irregularly alternate and situated near the middle of the lateral margin of the proglottides. The scolex attains a length of 144 μ and a breadth of 224 μ. Both the head and the suckers are unarmed and spines are also absent. The neck measures from 5 to 10 mm.

Muscular System. Immediately beneath the cuticle there is a layer of muscle fibres, internal to which there is a subcuticular longitudinal layer. More internally still there are well-developed longitudinal muscles.

The excretory system consists of two main longitudinal vessels situated laterally on each side.

The principal nerves run along the lateral margins of the body just internally to the inner longitudinal muscle fibres.

Male Genitalia. There are from 150 to 200 testes; of these from 100 to 125 are aporal, 30 to 50 poral and anterior to the

vas deferens, and from 20 to 30 poral and posterior to the vas deferens; they are all situated anteriorly to the ovary. The vas deferens in a mature proglottid commences as a coiled tube near the middle. The cirrus sac extends over one-sixth the breadth of the proglottid and measures from 128 to 192 μ.

Female Genitalia. The ovary is bilobed and granular; each lobe is made up of numerous elongated follicles, but in the posterior segments it becomes pear-shaped. The shell gland

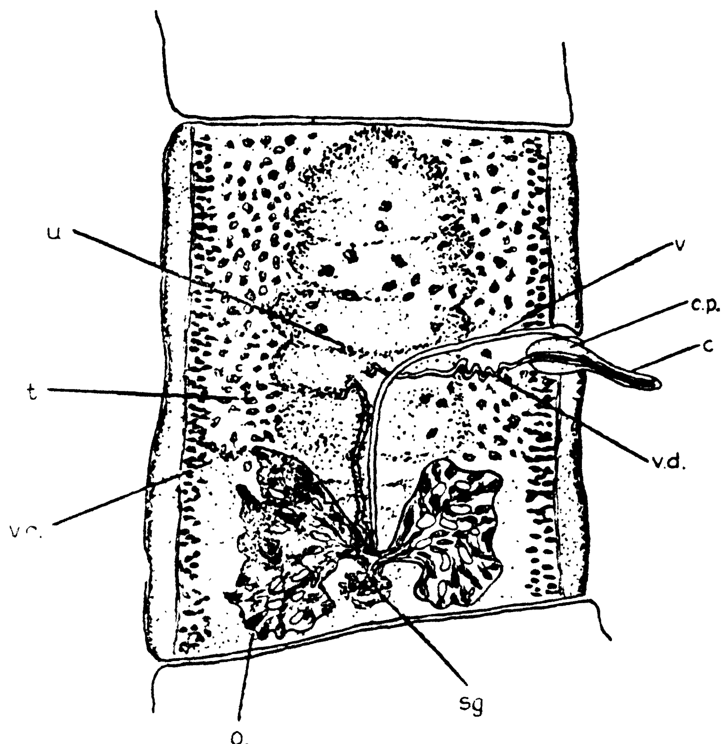


Fig. 211. *Proteocephalus ritæ.* Partly gravid segment. × 25. (After Verma.)

lies immediately behind the ovarian isthmus. Near the pore the vagina is slightly dilated and runs parallel and anteriorly to the vas deferens. Near the middle line of the segment it crosses the latter organ. The vitelline glands consist of numerous acini forming two lateral bands. The uterus bears from 8 to 12 diverticula on each side. The uterine egg measures 16 μ and the oncosphere 10 μ.

(8) **Proteocephalus woodlandi** Moghe, 1926. (Fig. 215.)

From *Calotes versicolor*, Nagpur, Central Provinces, India. Moghe.

The length of the worm is not known, but fragments measuring 3·1, 2·8, and 2·4 cm. were obtained. The genital pores are irregularly alternate and are situated behind the middle of the lateral margin of the segment. The scolex has a breadth of 525 μ and bears at its apex a fifth sucker; the cuticle of the scolex and of the anterior part of the worm is covered with minute spines. The largest segment has a breadth of 1·66 mm.

Male Genitalia. There are from 90 to 130 testes distributed, in mature segments, mostly in the two lateral fields; the central area, however, is not entirely free. There are none posterior to the ovary. The vas deferens is a stout, loosely-coiled tube situated dorsal to the excretory vessel. The cirrus sac measures 156 to 170 μ by 115 to 130 μ. It is sometimes anterior and sometimes posterior to the vagina, and

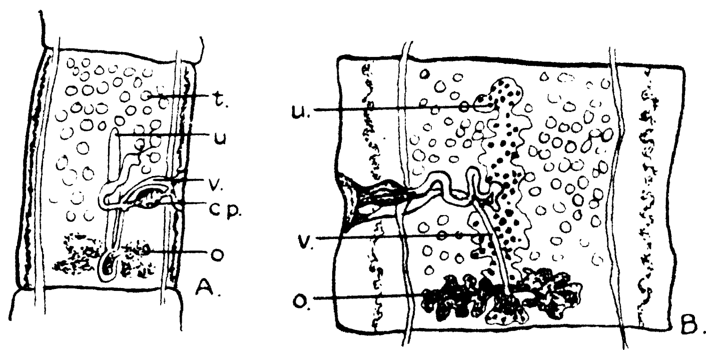


Fig. 215.—*Proteocephalus woodlandi.* A, mature segment, × 30; B, partly gravid segment, × 30. (After Moghe, in 'Parasitology.')

does not extend beyond the longitudinal excretory vessels. The cirrus is unarmed.

Female Genitalia. The ovary is situated at the extreme posterior margin of the segment and consists of two branching masses united by an ovarian bridge; it occupies more than half the width of the proglottid, and the poral is slightly larger than the aporal lobe. The vitelline glands extend the length of the segment along each lateral margin; they are situated in the cortex. The vagina varies considerably in size and appearance; close to the pore it is broad and muscular; in the inter-ovarian space there is sometimes a thin-walled dilatation; near the ovarian bridge it occasionally enlarges into a small curved receptaculum seminis. The

oviduct surrounds the shell gland. The uterus when fully developed consists of a central stem with from 10 to 12 diverticula on each side. The eggs measure 20 by 16 μ.

(9) **Proteocephalus fima** (Meggitt, 1927). (Fig. 216.)

Synonym :—*Crepidobothrium fima* Meggitt, 1927.

From *Rhabdophis stolatus*, Burma. Meggitt.

The length of the worm is not known, but it attains a maximum breadth of 1 mm. The gravid proglottides are much longer than broad, and the genital pores are situated a little in front of the centre of the margin of the segment. The

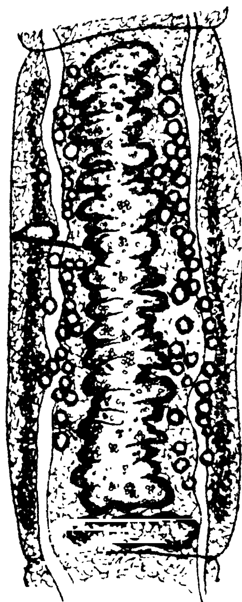


Fig. 216.—*Proteocephalus fima.* Nearly gravid segment, × 330 (After Meggitt.)

genital ducts pass between the longitudinal excretory vessels. The scolex has a diameter of about 200 μ and is not armed ; apical organ absent.

There are from 68 to 89 testes, of which from 33 to 54 are aporal and from 30 to 40 poral, *i. e.*, they are clearly separated into two lateral bands. The vagina may be either anterior or posterior to the cirrus sac, but it is usually anterior, and does not cross it. The uterus bears from 27 to 33 diverticula on each side.

(10) **Proteocephalus fixus** (Meggitt, 1927). (Fig. 217.)

Synonym :—*Crepidobothrium fixa* Meggitt, 1927.

From *Rhabdophis stolatus*, Burma. Meggitt.

The worm attains a length of 5 cm. and a maximum breadth of 1·5 mm. Gravid segments are longer than broad, the genital pores being situated in the centre of the lateral margin of the segment, but in gravid ones in the anterior third. The genital ducts pass between the longitudinal excretory vessels. The scolex is unknown. There are from 71 to 94

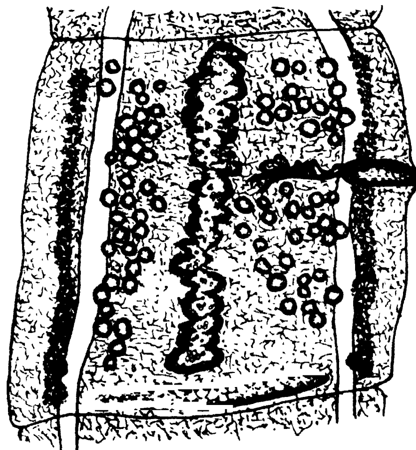


Fig. 217. *Proteocephalus fixus.* Mature segment, × 380. (After Meggitt.)

testes, of which 40 to 50 are aporal and 31 to 50 poral. They are disposed in two clearly separated lateral fields. The vagina as in *P. fima*. The gravid uterus bears from 20 to 24 diverticula on each side.

(11) **Proteocephalus vitellaris** (Verma, 1928). (Fig. 218.)

Synonym :—*Ichthyotænia vitellaris* Verma, 1928.

From *Bagarius yarrelli* (=*Pimelodus bagarius*), Allahabad, India. Verma.

The worm attains a length of at least 25 cm. and a maximum breadth of about 2·3 mm. It is composed of at least 700 proglottides; the genital pores are irregularly alternate and are situated near the middle of the lateral margin of the segment. The genital ducts pass between the longitudinal excretory vessels.

Muscular System. The longitudinal muscles consist of an indistinct external subcuticular and a thick internal layer; within the latter is a thin layer of circular muscles. Dorso-ventral fibres traverse the parenchyma.

The excretory system consists of the usual dorsal and ventral longitudinal trunks, all of the same size, on each side.

Male Genitalia. There are from 250 to 275 testes in a continuous dorsal field. The cirrus sac measures 250 by 140 μ, and extends from one-fifth to one-sixth the width of the segment. The cirrus is unarmed, and lies posterior to the vagina. The uterus has five diverticula on each side. The vitelline glands are L-shaped and lateral.

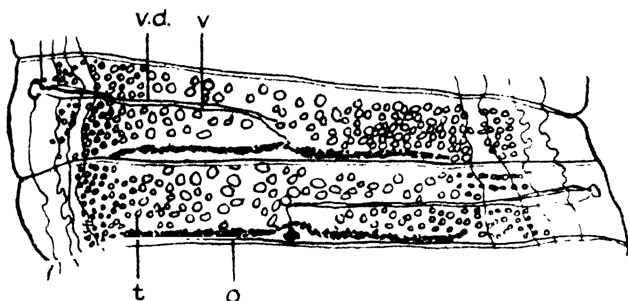


Fig. 218.—*Proteocephalus vitellaris.* Mature segments, × 32. (After Verma.)

SPECIES INQUIRENDÆ.

(12) **Proteocephalus** sp. (Southwell, 1922).

Synonym :—*Ophiotænia* sp. Southwell, 1922.

From *Bungarus cæruleus*, Zoological Gardens, Calcutta, India. Southwell.

Two immature worms without heads, each measuring about 1·5 cm. in length and 4 mm. in breadth, have been obtained from the above host.

Their identity is indeterminable.

(13) **Proteocephalus** sp. (Meggitt, 1926).

Synonym :—*Acanthotænia* sp. Meggitt, 1926.

From *Bungarus fasciatus*, Rangoon, Burma. Meggitt.

Meggitt (1926) recorded this undetermined larval species from the above host.

(14) **Proteocephalus** sp. (Meggitt, 1927).

Synonym :—*Crepidobothrium* sp. Meggitt, 1927.

From *Oligodon purpurescens*, Burma. Meggitt.

Meggitt records from this host a single immature specimen which, owing to the absence of genital organs, could not be identified. It measured 1·2 mm. in length and 270 μ in breadth. The scolex had a diameter of 250 μ and an apical organ was absent.

Genus II. GANGESIA Woodland, 1925.

In this genus the scolex bears a rostellum armed with hooks.
Type-species:—*Gangesia bengalensis* (Southwell, 1913)

Key to Species.

1.	Hooks all of same size	2.
	Hooks of different sizes	*G. macrones*, p. 382.
2.	Hooks 30 to 44 μ in length	*G. bengalensis*, p. 382.
	Hooks 52 to 60 μ in length	*G. pseudeutropii*, p. 384.

(1) Gangesia bengalensis (Southwell, 1913). (Fig. 219.)

Synonyms:—*Ophryocotyle bengalensis* Southwell, 1913.
Gangesia wallago Woodland, 1924.
Gangesia agraensis Verma, 1928.

From (1) *Ophiocephalus striatus*, *Labeo rohita*, and *Wallago attu*, Bengal, India. Southwell. (2) *Wallago attu*, Rivers Ganges and Jumna, Allahabad, United Provinces, India. Woodland; Verma.

The worm attains a length of about 7 cm. and a maximum breadth of about 1·8 mm.; usually, however, it is less than half this size. It consists of from 100 to 200 segments, all of which are broader than long except a few of the more posterior ones. The genital pores are irregularly alternate and situated anteriorly to the middle of the lateral margin of the segment; no uterine pores have been discovered. The scolex measures from 166 to 232 μ in length and from 298 to 488 μ in breadth; the anterior two-thirds of the margin of the suckers is armed with numerous spines each measuring about 7 μ in length. A distinct rostellum is present, and bears from 28 to 42 hooks arranged in a single row, each hook measuring from 30 to 44 μ in length.

Male Genitalia. There are over 100 testes in one continuous field several layers deep in the medulla, and situated anteriorly to the ovary and between the lateral vitellaria. The cirrus sac normally extends one-third the distance across the segment and measures about 230 μ in length; it is sometimes anterior and sometimes posterior to the vagina.

Female Genitalia. The ovary is posterior and bilobed, the two halves being joined by an isthmus. The uterus bears from 20 to 28 lateral diverticula on each side. The egg measures from 92 to 99 μ and the hookless embryo from 18 to 22 μ.

(2) Gangesia macrones Woodland, 1924. (Fig. 220.)

From *Macrones seenghala*. Rivers Ganges and Jumna, Allahabad, United Provinces, India. Woodland.

The worms measure from about 2·8 to 5·6 cm. in length and

have a maximum breadth of about 1 mm. They are composed of from 150 to 200 proglottides. The genital pores are irregularly alternate and are situated anteriorly to the middle of the lateral margin of the segment. No uterine pores have been discovered. The scolex measures about 110 μ in length and 194 μ in breadth. It bears a conspicuous, spherical, muscular rostellum having a diameter of 110 μ, and bearing on its upper

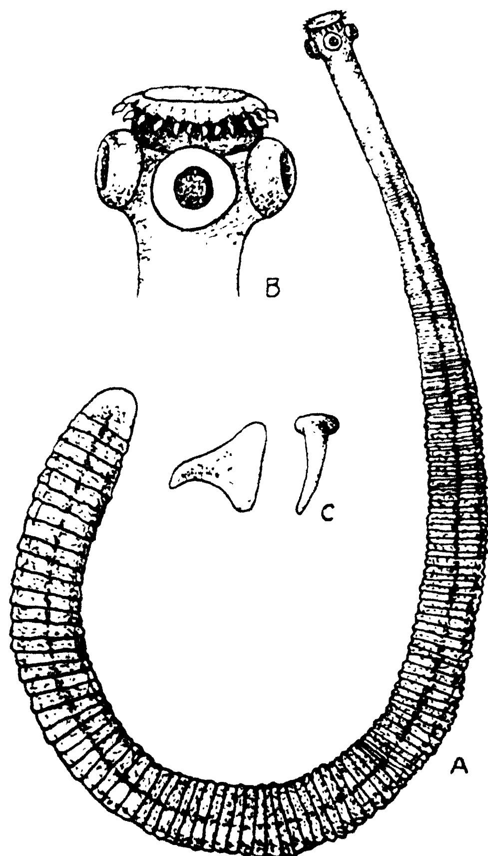


Fig. 219.—*Gangesia bengalensis*. A, entire worm, about × 30; B, head, × 100; C, hooks, magnification unknown. (After Southwell.)

half about 33 hooks arranged in a single complete ring; the hooks are of two kinds, large and small, which alternate with each other; the larger measure from 11 to 14·6 μ, the smaller being about half this size. The upper two-thirds of the margins of the suckers bear numerous minute spines. There is no neck.

There are over 100 testes arranged in one continuous field anteriorly to the ovary and between the vitelline glands. The cirrus sac usually opens anteriorly to the vagina, but the reverse may be the case. The sac extends from one-sixth to one-quarter the breadth of the proglottis, and it contains a few

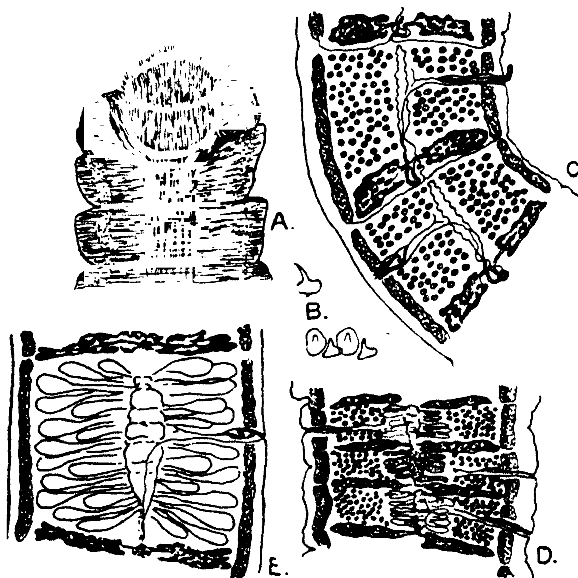


Fig. 220.—*Gangesia macrones.* A, head, × 120; B, rostellar hooks, × 350; C, mature segment, × 12; D, partly gravid segment, × 12; E, gravid segment, × 12. (After Woodland, in 'Parasitology.')

coils of the vas deferens. The ovary is bilobed, the lobes being connected by a very thin isthmus. The vagina sometimes joins the oötype from the right side and sometimes from the left. The uterus consists of a central stem with from 20 to 30 lateral diverticula on each side.

(3) **Gangesia pseudeutropii** Verma, 1928. (Fig. 221.)

Synonym:—*Gangesia pseudotropii* Verma, 1928

From *Pseudeutropius garua* (=*Silurus garua*), Allahabad, (Ganges and Jumna). Verma.

The worm attains a length of from 2 to 4 cm. and a maximum breadth of 1 mm. It contains from 20 to 40 proglottides, the posterior ones being much longer than broad. The genital pores are situated behind the middle of the lateral margin of the segment. The neck and strobila are covered with minute spines.

Muscular System. This consists of an outer band of longitudinal muscles occupying the entire subcuticular area, the inner longitudinal layer consisting of a slender band of scattered fibres. The circular muscles are weakly developed. The ventral excretory vessels are larger than the dorsal ones. The scolex measures about 190 μ in length and 240 μ in breadth. The rostellum bears an apical organ armed with from 17 to 20 hooks, each of which has a length of from 52 to 60 μ.

Male Genitalia. There are from 100 to 160 testes arranged in two lateral fields and situated in front of the ovary. The cirrus sac measures from 225 to 260 μ by 65 to 100 μ; it passes

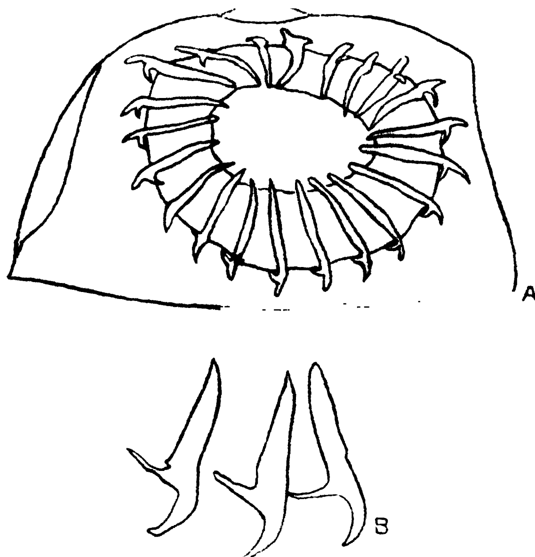


Fig. 221.—*Gangesia pseudeutropii.* A, head, ×260 B, rostellar hooks, ×500. (After Verma.)

between the dorsal and ventral excretory vessels; the vas deferens, on leaving the sac, becomes much coiled.

Female Genitalia. The ovary is bilobed and situated posteriorly. The ovejector is well developed and measures 60 μ. The vitelline glands consist of a longitudinal lateral band on each side of the segment, not extending anteriorly to the genital pore, but the aporal is slightly longer than the poral band. The uterus bears from 30 to 40 lateral diverticula on each side. The egg measures about 35 μ and the embryo 13 μ. Verma states that the latter develops a bladder having a diameter of about 160 μ and also a neck whilst still in the detached gravid segment in the rectum of the host.

ALPHABETICAL INDEX.

[Names printed in *italics* are synonyms.]

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